DEVELOPMENT OF POPULATION DIALLEL CROSS OF PEARL MILLET ELITE COMPOSITES

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ABSTRACT

Information on heterosis and combining ability is derived from data on nine agronomic traits (grain yield per season, grain yield per day, time to flowering, plant height, panicle length, biomass, growth index, tiller number, and thousand seed mass) from a diallel cross involving eleven diverse pearl millet (*Pennisetum glaucum*) populations of African and Indian background developed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). The populations, along with their crosses (excluding reciprocals), were grown in a randomized complete block design with three replications across five environments in India (Patancheru and Bhavanisagar 1993 rainy season, Patancheru 1994 dry season, and Patancheru 1994 and 1995 rainy seasons). The objectives of this study were to evaluate the combining ability of these populations and to explore the potential for their utilization in interpopulation improvement for the development of high yielding composites with a broad genetic base.

Significant differences among entries for most traits were observed. Parental population effects (V_i) were significant for all traits whereas heterosis effects (h_{ij}) were significant for grain yield per season, time to flowering, panicle length, tiller number, and thousand seed mass. Average heterosis effects ($\bar{h}$) were nonsignificant for most traits indicating the absence of dominance genetic effects for these traits. The genetic parameters estimated by the Gardner-Eberhart method provide indirect evidence on gene action as dominance and additive genetic effects were determined jointly. The large variety effects and the significant variety heterosis (h_i) together with the magnitude of general combining ability (GCA) suggested predominance of additive genetic effects for all traits studied. These results revealed that considerable genetic variability exists in the eleven parental populations for a number of traits, and much of this variation was additive in nature.

The parental populations having good performance per se and good performance in crosses for most traits were ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059. These

populations are more suitable for intercrossing to develop new populations with good agronomic performance and increased genetic variability to be exploited in a recurrent selection program to generate high-yielding open-pollinated pearl millet varieties. Based on the high proportion of additive effects suggested in this study for most traits it should be possible to efficiently utilize the large genetic variability of pearl millet populations from India and Africa by intrapopulation breeding through recurrent selection. Such an approach should allow combination of high yields with other desirable traits. The current results suggest that ICMV 91059, SenPop, and ICMP 92591 would be the best populations to initiate a short-term breeding program with their significant variety effects and positive GCA and high mean yield performance. Alternatively, a broad based population could be developed for longer-term recurrent selection using ICMV 155, ICMP 87307, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059, the best parents for mean yield per se and in crosses, and good combiners for earliness, short plant height, and bold grain size. ICMP 87200 was especially excellent for grain yield when crossed with ICMV 91059. This cross had the highest grain yield per season (3220 kg ha^{-1}) among all entries including controls. Finally, as ICMV 91059 is thought to be only remotely related to the other superior parental populations, it could prove advantageous in the long run for hybrid development to form two populations--one based on ICMV 91059 and the other based on the remaining two to five selected parental populations.

بسم الله الرحمن الحيم

إنتاج هجن جديدة من عشائر الدخن الصفوة باستعمال تصميم دايالليل

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الخلاصـــة

المعلومات عن قوة الهجين والقدرة على الخلط أخذت من معطيات تسع صفات محصولية (انتاج الحبوب في الموسم، انتاج الحبوب في اليوم، الوقت المطلوب للأزهار، طول النبات، الكتلة الحيوية. معدل النمو، عدد الخلف ووزن الالف حبة) نتيجة استعمال تصميم دايالليل لتهجين أحدى عشر عشيرة مختلفة من الدخن ذات أصول هندية وأفريقية طورت بواسطة المعهد الدولي للمناطق الاستوائية شبه الجافة (ICRISAT). عشائر الآباء والجيل الأول الناتج عن تهجينها مع بعضها البعض (٦٦ مدخل) ما عدا التهجين الرجعي أدخلت في تجربة على هيئة المربعات العشوائية الكاملة في ثلاث مكررات تحت خمس بيئات مختلفة في الهند (بتانشيرو وباوانصقر في خريف ١٩٩٣م بتانشيرو، صيف ١٩٩٤م وبتانشيرو خريفي ١٩٩٤، ١٩٩٥م). أهداف هذ الدراسة هي تقييم قدرة هذه العشائر على الخلط و معرفة مدى إمكانية استخدمها في انتاج هجن متعددة السلالات للوصول إلى أصناف ذات انتاجية عالية ومبنية على قاعدة وراثية عريضة.

أوضحت هذه الدراسة وجود تباين معنوي بين المداخل لمعظم الصفات. أثر عشائر الآباء معنوي لكل الصفات بينما قوة الهجين معنوية فقط لانتاج الحبوب في الموسم، الوقت المطلوب للأزهار، طول القندول، عدد الخلف ووزن الألف حبة. متوسط أثر قوة الهجين غير معنوي لمعظم الصفات مما يدل على غياب العوامل الوراثية السائدة لهذه الصفات. تقدير العوامل الوراثية بطريقة قاردنر – ابرهارت أظهرت دليل غير مباشر عن الفعل الجيني لأن العوامل الوراثية السائدة والأضافة حددت مجتمعة. الأثر المعنوي الكبير للعشيرة (الآباء) بالاضافة للقدرة العامة على الخلط تدل على طغيان التأثير الاضافي في توريث الصفات موضوع الدراسة. أظهرت نتائج الدراسة وجود تباينات وراثية كبيرة بين عشائر الآباء في عدة صفات وثبت بأن معظم هذا التباين له طبيعة اضافية في التوريث.

عشائر الآباء التي أظهرت أداء ذاتي ممتاز وأيضاً أداء جيد في الجيل الأول لأغلب الصفات هي ICMV 155, ICMP 91751, ICMP 92591, SenPop و ICMV 91059. هذه العشائر مناسبة

للتهجين مع بعضها لتكوين وتطوير عشائر جديدة ذات صفات محصولية جيدة وتباينات وراثية يمكن استغلالها في برامج التربية باستعمال الانتخاب المتكرر لانتاج أصناف مفتوحة التلقيح ذات انتاجية عالية. نسبة للأثر الكبير للفعل الاضافي في توريث هذه الصفات الذي ثبت من خلال الدراسة فانه بالامكان استخدام التباين الوراثي الكبير الموجود في عشائر الدخن الهندية والأفريقية بكفاءة عالية في التربية لتهجين العشائر مع بعضها باستخدام الانتخاب المتكرر. مثل هذه الطريقة تسمح بمزج صفات الانتاجية العالية مع الصفا ت الأخرى المرغوب فيها . النتائج الحالية أظهرت أن SenPop, ICMV 91059 و ICMP 92591 يمكن أن تكون أحسن العشائر لقيام برنامج تربية قصير المدى لتأثيرها المعنوي وقدرتها العامة على الخلط وارتفاع متوسط انتاجها. بديلا عن ذلك يمكن انتاج عشيرة ذات قاعدة وراثية عريضة لكي يتم تطويرها باستخدام برنامج الانتخاب المتكرر طويل المدى مستخدمين SenPop, ICMP 92591, ICMP 91751, ICMV 155 و ICMV 91059 وهي أفضل العشائر من ناحية انتاجيتها وانتاجية الهجن الناتجة عنها، ولها قدرة عالية على الخلط لصفة التبكير وقصر النبات وكبر حجم الحبوب. الهجين الناتج عن ICMP 87200 و ICMV 91059 أعطى انتاجية أعلى من كل المداخل بما فيها الشواهد (٣٢٢٠ كجم للهكتار). بما أن ICMV 91059 هي الوحيدة التي لا ترتبط وراثياً مع عشائر الآباء الصفوة المنتقاة فهذا يثبت خصوصيتها الايجابية للمدى البعيد لانتاج نوعين من العشائر، الأول مبني على هذه العشيرة والاخر مبني على بقية العشائر المنتخبة من الاباء.

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LIST OF ABBREVIATIONS

Abbreviation	Meaning
BM	biomass
C_4	fourth cycle of selection
cm	centimeters (length or height)
cm^2	square centimeters
°C	degrees Celsius
d	days
DAE	days after emergence
ERC	Ergot Resistant Composite
et al.	*et alii*, (and others)
FAO	Food and Agriculture Organization
F_1	first generation after a cross
g	grams
GCA	general combining ability
GI	growth index
GYPD	grain yield per day
GYPS	grain yield per season
h	hours
ha	hectares
HCP	head count per plot
HI	harvest index
h^2	narrow sense heritability
IAC	ICRISAT Asia Center
ICMP	ICRISAT millet population
ICMS	ICRISAT millet synthetic
ICMV	ICRISAT millet variety
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IVC	Intervarietal Composite
kg	kilograms
kg ha^{-1}	kilograms per hectare
LHGP	Long Headed GenePool

Abbreviation	Meaning
m	meters
MC	Medium Composite
mm	millimeters
MS	Mean Squares
m^2	square meters
n	number of parents
NARS	National Agricultural Research Systems
NELC	New Elite Composite
NWC	Nigerian World Composite
P	Probability of a greater value of F or r resulting from chance alone
P.	*Pennisetum*
p.	page
PCP	plant count per plot
PH	plant height
PLN	panicle length
pp.	pages
r	Pearson's rank correlation coefficient
RBD	randomized block design
SCA	specific combining ability
SRC II	Smut Resistant Composite II
SYD	straw yield
TFL	time to 75% flowering
TNO	Tiller number
TSM	Thousand seed mass
vs.	versus
x	crossed with or multiplied by
>	more than
≥	more than or equal
<	less than

Introduction

INTRODUCTION

Pearl millet is scientifically known as *Pennisetum glaucum* (L.) R. Br. [syn *P. americanum* (L.) Leeke and *P. typhoides* (Burm.) Stapf & Hubbard]. Other common names for this crop are cattail millet or bulrush millet in English, bajra in Hindi and dukhn in Arabic. Pearl millet is a C_4 species with a very high photosynthetic efficiency and dry matter production capability. It is grown annually on about 26 million hectares in the arid and semi-arid tropics of Africa and the Indian subcontinent, principally for food grain but also for fodder, feed, and fuel (Rachie and Majmudar, 1980; Anand Kumar, 1989). It is also grown on small scale as a high quality forage crop in the USA, India, Australia, South America, and southern Africa. In regions characterized by low erratic rainfall, high temperatures, low inherent soil fertility, and numerous biotic stresses, the crop has advantages over sorghum (*Sorghum bicolor* (L.) Moench) and maize (*Zea mays* L.) due to its higher and more stable grain yields (Burton and Powell, 1968; Burton, 1983; Anand Kumar, 1989).

Pearl millet is predominantly grown under severe droughty conditions, and in sandy soils having low cation exchange capacity. Pearl millet is better adapted than other cereals to such adverse environments due to its ability to withstand high temperatures and severe moisture deficits, yet recover rapidly to fully exploit favorable conditions and give high yield. This environment typifies that of the Sudanian zone of western and central Africa including the western region of Sudan where the crop is dominating. Although the nutritional value of the crop is high (protein ranges between 13 and 17%) (Rachie and Majmudar, 1980), average grain yields both in Africa and the Indian subcontinent are low (500-600 kg ha^{-1}) (Anand Kumar, 1989). Increasing the productivity of pearl millet in such low-yielding and unpredictable environments, to keep pace with

the increasing food demand of the growing population in these regions, is a very big task requiring cooperative efforts from national and international research and development organizations. Poor harvest index of landraces in Africa is recognized as an important attribute requiring genetic improvement for increasing the grain yield potential of this crop. The traditional landraces are often tall, have thick stems, and are excessively leafy. While the biomass production of these landraces under the prevailing low-resource farming systems is very high (6-12 t ha^{-1}), their harvest index is often below 20% as compared to over 30% for improved cultivars with high grain yield potential (Anand Kumar, 1989).

Pearl millet is a highly cross-pollinated crop with immense genetic diversity, and hence is amenable to genetic improvement by the recurrent selection methods used in other cross-pollinated crops such as maize. It has several additional features, viz., bisexual and protogynous flowers, large number of seeds (up to 3000 per panicle), excellent tillering ability (4 to 6 tillers $plant^{-1}$ under wide spacing and good management), and low seed rate (3 kg ha^{-1}), that make pearl millet especially suitable for genetic improvement by recurrent selection. Recurrent selection is the cyclical upgrading of open-pollinated varieties, synthetic varieties, and composites formed from a mixture of landraces, varieties, and inbred lines. Improved populations may be used either as source populations for new inbred lines or directly used by farmers as open-pollinated varieties. The former use is for more advanced programs, whereas the latter is for developing areas, such as Sudan, that do not have the means for timely production and distribution of fresh hybrid seed to farmers for sowing each season. In pearl millet, improved populations have been used to breed open-pollinated varieties and to derive inbred parental lines for hybrid breeding programs. The advantages of open-pollinated varieties over hybrids are that their seed multiplication is cheaper and quicker, their

disease resistance is more stable over seasons and locations, and farmers can maintain their own seed stocks and improve local adaptation of open-pollinated varieties by mass selection.

In the current study, an inter-varietal diallel cross of 11 open-pollinated varieties and recurrent selection population bulks of pearl millet has been developed and evaluated at ICRISAT Asia Center (IAC) with the intention of using the Gardner and Eberhart (1966) Analysis II to evaluate the performance of these varieties in crosses. The parents and their n(n - 1)/2 F_1 crosses (total of 66 entries) were included in 1993 trials at two locations in India (Patancheru and Bhavanisagar), the following 1994 summer off-season at Patancheru and with selfed progenies of the parents and crosses (total of 131 entries) in the 1994 and 1995 rainy seasons at one location (Patancheru). The crosses and the evaluation of this material for two seasons (1993 & 1994) were carried out by pearl millet breeding program of IAC (C. Tom Hash). I repeat this experiment in 1995 rainy season and data collected on different traits.

The objectives of this study were to measure and evaluate combining ability and heterosis among eleven different pearl millet populations and to explore the potential for their further utilization in population improvement for the development of high yielding composite varieties for the semi-arid tropics. The ultimate objective of this research is to develop one or two new populations having high mean agronomic performance and broad genetic base to serve as sources of improved varieties and inbred lines which can be obtained by recurrent selection.

Review of Literature

REVIEW OF LITERATURE

The objective of this review is to present previous findings on pearl millet and related crops concerning the diallel mating design with emphasis on variety diallel crosses related to the objectives outlined for this study. Literature on diallel mating designs in pearl millet and related cross-pollinated crops are briefly reviewed to throw some light on breeding methods and objectives of pearl millet useful for designing future strategies aimed at improving production and productivity of this crop.

Pearl millet

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is a cereal grain crop that grows as a robust annual bunch grass. It can produce seed when grown on soils that are too acid, dry, or infertile for sorghum and maize (Burton and Powell, 1968) and, thus, it is commonly sown in semi-arid regions. Pearl millet is the predominant crop in northwest India and the Sahel of Africa (Brunken *et al.*, 1977; Rachie and Majmudar, 1980; Pearson, 1985). Selection for adaptation to moisture stress probably is responsible for its rapid and deep rooting capacity (Begg, 1965; Gregory and Squire, 1979), and its efficient use of water (Kassam and Kowal, 1975), and its ability to produce viable seed when water scarcity stops grain filling prematurely (Fussell and Pearson, 1980). The earliest human effort to increase grain yield of this crop may have involved mass selection for well filled-panicles, panicle compactness, panicle length, and high seed weight (Krishnaswamy, 1962).

Pearl millet is an outcrossing crop with immense genetic diversity. Its panicles vary in length from 5 to 150 cm (Burton and Powell, 1968) and it varies considerably in tillering habit (Raymond, 1968). Many land races of millet exist (Brunken *et al.*, 1977; Norman *et al.*, 1984). Isozyme analyses have shown that early and late West African varieties are genetically distinct even when collected from the same village (Tostain *et al.*, 1987). Genetic variation for grain yield of millet is shown in crosses between adapted parents (Khadr, 1977; Sandhu *et al.*, 1980; Sachdeva *et al.*, 1982) and crosses between adapted and wild, weedy, or landrace accessions (Gupta and Singh, 1973; Bramel-Cox *et al.,* 1987).

Phenotypic expression of pearl millet traits can be greatly altered by environmental factors. For example, plant height can be reduced drastically by moisture stress (Burton and Powell, 1968) and both panicle number per plant and tiller size are reduced by high plant density (Carberry *et al.*, 1985). Virk *et al.* (1984) found that grain yield varied from 429 to 3123 kg ha^{-1} over 19 locations in India. Further, genotype x environment interactions can contribute to phenotypic differences. For example, varietal rankings for days to bloom can be inconsistent over several day length or temperature regimes (Begg and Burton, 1971), and genotype x location and genotype x nitrogen level interactions have occurred for grain yield (Sachdeva *et al.*, 1982; Nwasike *et al.*, 1983).

Heritability values for grain yield, yield components, and morphological traits of pearl millet may be high (Pokhriyal *et al.,* 1967; Gupta and Nanda, 1971; Sangha and Singh, 1973), low (Gupta and Athwal, 1966) or variable (Burton, 1951). Generally, heritability

values are high when based on data from a single environment but low when based on data from two or more environments (Singh, 1974; Sandhu *et al.*, 1980).

Population improvement

Population improvement has been developed as an important method of breeding cross-pollinated crops and has been exploited recently in pearl millet to improve yield potential of some populations (Gill *et al.*, 1978; Gupta and Andrews, 1978). It is based on frequent hybridization and continuous selection to generate and exploit genetic variability in the base populations through various recurrent selection procedures. The improved population can be used as a new variety and/or as a base material to derive inbred lines for use in hybrid combinations. The success of a breeding program largely depends upon the appropriate choice of the base material, breeding method and type of variety to be developed. To arrive at these conclusions, the plant breeder is guided by the genetic parameters providing information about variability, type of gene action, and the potential of the base material. The estimation of additive and nonadditive components of genetic variance depends largely on gene frequency and gene effects.

Nature of gene action

Knowledge of various types of gene action and their relative magnitudes in controlling various traits is basic to maximizing efficiency of a breeding program. Genetic variation in pearl millet has been partitioned into additive, dominance, and epistatic effects using different types of mating designs. Estimates were obtained from line x tester analysis,

diallel crosses, and North Carolina (NC) designs (Gill, 1991). The gene action has also been obtained by combining ability analysis in which σ^2_{gca} is equated to half the additive variance plus the additive x additive type of epistasis and σ^2_{sca} to dominance plus dominance x additive and dominance x dominance types of epistasis (Falconer, 1981; Hallauer and Miranda, 1988; Gill, 1991).

Nonadditive gene action is a significant source of genetic variation for pearl millet grain (Kapoor *et al.*, 1982; Sachdeva *et al.*, 1982; Tyagi *et al.*, 1982) and straw fodder yields (Burton, 1959, 1968; Begg and Burton, 1971). Narrow sense heritability (h^2) is smaller than broad sense heritability for harvest index, grain fill period, tiller number, and leaf width (Lal and Singh, 1970; Bajaj and Phul, 1982), which suggests that nonadditive gene action is important for these traits. In contrast, panicle length and diameter are determined primarily by additive gene action (Jain *et al.*, 1961; Gupta and Singh, 1971).

Positive correlation of pearl millet grain yield with tiller number (Jindla and Gill, 1984; Singh *et al.*, 1980), days to flower, threshing percentage (Nwasike *et al.*, 1983), seed weight (Sangha and Singh, 1973), and straw yield (Pokhriyal *et al.*, 1967) have been reported. Pearl millet grain yields have been predicted by using optimum indices (Shankar *et al.*, 1963) and indices based on multiple regression (Gupta and Athwal, 1966; Mahadevappa and Ponnaiya, 1967; Singh and Ahluwalia, 1970; Phul *et al.*, 1974).

Parent-offspring heritability values reported were generally highly significant for all traits but varied greatly in magnitude. Values range from 0.46 to 0.64 for panicle size and seed traits, from 0.27 to 0.58 for productivity traits, and from 0.16 to 0.32 for

partitioning traits, when averaged over three pearl millet composites (Rattunde *et al.*, 1989).

Earliness and lateness were studied in crosses among early Tifton lines and late, short day lines. Genetic analysis of the anthesis data revealed little dominance for earliness or lateness (Burton, 1965). Burton (1965) reported photoperiodism in certain pearl millet introductions from Nigeria and Upper Volta. Carberry *et al.* (1985) found that as photoperiod increased from 13.5 to 15.5 h, time taken to panicle initiation increased from 16 to 34 days.

Singh and Murty (1974) obtained estimates of additive and dominance components of genetic variance for five characters: synchrony of tillering, days to 50% heading, tiller number, grain yield, and test weight. Using the hierarchial system proposed by Horner *et al.* (1955), revealed the magnitude of the additive component was low compared to the dominance component of genetic variance for all traits examined. The magnitude of dominance variance was highest for grain yield. The low magnitude of additive genetic variance was probably due to the highly selected nature of the parents for yield and other characters, which might have resulted in the fixation of genes controlling these characters at many loci.

Rachie and Majmudar (1980) suggested that the large component of nonadditive genes can be exploited by developing new hybrids using suitable recombinants of biparental progenies. Singh *et al.* (1972) observed that additive, dominance, and dominance by dominance gene effects played a significant part in the inheritance of most characters in two crosses of pearl millet.

Ahluwalia and Patnaik (1963) studied heterosis in hybrids among four Indian, five Rhodesian, and two Ghanaian lines. Nineteen of the resulting hybrids were examined, and five showed heterosis for grain yield. Heterosis for earliness and negative heterosis for spike length and grain weight were also observed. The two Ghanaian testers IP 80 and IP 81, were found to have good general combining ability.

Andrews *et al.* (1985b) exploited variability from African germplasm for disease resistance, panicle volume, and seed size in crosses with Indian materials. They pointed out that African parentages occur in nearly all of advanced breeding products of the ICRISAT pearl millet improvement program. Among the African material, early groups have proved more promising in crosses at ICRISAT than late, photosensitive groups. The early groups of pearl millet are known locally in West Africa, as 'Gero' or 'Souna' and the late ones as 'Sanio' and Maiwa'. Recurrent selection has been used to produce open-pollinated cultivars, one of which, WC-C75 (also named by ICRISAT as ICMV 1) was developed from the "World Composite" by recurrent selection and released in 1982 by the government of India for general cultivation as a commercial open-pollinated cultivar (Andrews *et al.*, 1985a). More recent products of recurrent selection at ICRISAT Asia Center (IAC) include ICMV 155, an open-pollinated cultivar developed at IAC from the "New Elite Composite" and released in 1991 for use in all millet growing areas of India (Pheru Singh *et al.*, 1994), and ICMV 88908, an open-pollinated cultivar based on selection and crossing within the Bold Seeded Early Composite at IAC and released in Namibia in 1990 as Okashana-1 (Witcombe *et al.*, 1995). Inbred products include ICMP 423 the downy mildew resistant restorer line of single-cross hybrid cultivar ICMH 423,

was developed at ICRISAT by selection within its Early Composite and released in India in 1988 (Rai *et al.*, 1994), and ICMP 451, restorer parent of the single-cross hybrid cultivar ICMH 451 that was developed at IAC from the Late Composite and released in 1986 (Anand Kumar *et al.*, 1995). Conventional pedigree has been used to produce synthetic parents, pollinators and seed parents.

Growth index

Growth index (GI) is the measure of plant dry weight produced per unit land area per day (grams per square meter per day). Lynch *et al.* (1995) studied the inheritance of Growth Index (GI) for pearl millet. They found that additive genetic effects were more important for GI1 (GI at 10 d after bloom date), bloom date, harvest index, and plant height, whereas additive x additive epistatic effects were of greatest importance for biomass and GI2 (GI at maturity).

Inbreeding depression

Selfing pennisetums invariably leads to inbreeding depression, with restoration of vigor on outcrossing. The general decline in rate of growth, plant development, and other characters is often accompanied by the appearance of occasional "defective" such as dwarfs, and of chlorophyll deficiencies, low fertility, and reduced plant height, head length, and thickness (Kadam *et al.*, 1940; Pandya *et al.*, 1956; Pokhriyal *et al.*, 1966).

Nambiar and Menon (1955) observed that there was reduction in most morphological characters except for number of tillers and number of heads per plant. Rachie *et al.*

(1967) developed large numbers of highly vigorous dwarf inbreds by a system of frequent recombination followed by intensive selection under different environments. One of these dwarf inbreds, D 174, was vigorous enough to become a potential variety under certain conditions (Bakshi *et al.*, 1966). This suggests that favorable gene action can be accumulated into homozygous genotypes if the selection options are high enough (sufficient numbers of segregating plants), if recombination occurs often enough to provide the basis for reassortment of characters, and if enough generations are grown to permit reassembling desirable linkages.

The level of inbreeding is apparently not related to combining ability. Krishnaswamy (1962) observed that high-yielding inbreds did not always produce good combiners, and sometimes weak inbreds were high combiners. It also affects seed setting. Burton (1952) found that 74 open-pollinated plants produced only 901 mg of seed per 5 cm of head length when selfed, and 1343 mg of seed per 5 cm when topcrossed, a highly significant difference. Moreover, continued inbreeding reduced both seed size and number of seed set. Rai *et al.* (1985) examined the effects of one generation of selfing on grain yield, plant height, head length, 1000 seed weight, and days to flowering in the Medium Maturity Composite and Serere Composite-1 of pearl millet. Results showed that average inbreeding depression in both composites was highest for grain yield (25% and 36%) followed by 1000 seed weight (12% and 14%). Plant height, days to flowering and head length were least affected by selfing, with average inbreeding depression for these characters ranging from 4% to 7%.

Analysis of a Diallel Cross

Diallel mating design is a type of mating systems in which a fixed set of parents are crossed in all possible combinations, and the number of crosses equal to n(n - 1)/2 excluding reciprocals. Plant breeders have often used the diallel cross to investigate the genetic properties of a group of populations. Hull (1945), Yates (1947) and Griffing (1950) proposed ways of analyzing the results of a diallel cross. Jinks and Hayman (1953), Hayman (1954a, 1954b) and Jinks (1954) developed a method of analysis that has been widely used for evaluating the mode of gene action (Dwivedi *et al.*, 1980; Koevering *et al.*, 1987; Powell, 1988). This analysis is based on a model that, for any locus i with two alleles, the difference between the two homozygotes is $2d_i$, whereas d_i is the dominance deviation. The difference between the heterozygote and the mid-homozygote value is h_i, while the frequency of the two alleles is U_i and V_i.

Christie and Shattuck (1992) concluded that if the parents utilized in the diallel represent a random sample from a population, the result can be applied to that population (random model). The reference population must be in genetic equilibrium (i.e., Hardy-Weinberg and linkage equilibrium) and must be random mating with no selection. One can visualize such a population in species that reproduce by cross-pollination. However, the Hayman and Jinks analysis has been utilized mainly in self-pollinating species, and in that case it is difficult to visualize highly selected parents from a progressive breeding program representing a random sample of a population.

Johnson (1963) used the fixed model and Baker (1978) suggested that it was the only appropriate model. Unlike Griffing's analysis (1956b), the model is not critical of the Hayman and Jinks analysis.

Hayman (1958) found that measurement of additivity and dominance in the presence of epistasis is problematic. He concluded that this difficulty can be avoided by finding the best-fitting non-epistatic model and considering its deviation from observation in terms of the epistasis present.

Jinks and Hayman (1953) showed how to obtain various measures of gene frequency and gene action from a diallel table. Heterozygosity per se has been described as a source of heterosis by several writers, e.g. Jinks and Mather (1955) for the character stability.

Kempthorne (1956) has questioned the value of derived statistics unless they can be applied to some population. Wright (1985) has provided a thorough discussion of the reference population for a diallel. Very briefly, he defines the reference population in the usual way (random mating, no selection, genetic equilibrium) and defines two types: ancestral and descendent. Christie and Shattuck (1992) defined the two population as follows:

1) The ancestral reference is the one from which the parents of the diallel represent a random sample. The parents may be taken directly from the population, or derived by inbreeding without selection.
2) The descendent reference population is a population that would be developed from the diallel parents by several generations of random mating. This represent the

traditional fixed model. Wright (1985) goes on to discuss some implications for these two models, specially the role of S_1 progenies in derivation of estimates.

The appropriateness of the kinds of diallel crossing methods depends on the experimental material and the objective of the experiment. If the experimental material can be assumed to be a random sample from a random mating population, genetic interpretations may be given to the combining ability statistics (Griffing, 1956a). Griffing (1956a) indicated that estimation of the additive and nonadditive genetic variances require that a chain of assumptions be met. He pointed out that to obtain unbiased estimates, diallel crossing method 3 or 4 (see p. 15 below) must be used (i.e. the parents are not included in the combining ability analysis). He concluded that diallel crossing systems may be used in at least two broad and related fields, namely, those of plant and animal breeding, and quantitative inheritance.

Christie and Shattuck (1992) attributed the criticisms of diallel analysis, and perceptions of abuse, to the interpretations made from the results. They pointed out that the plant breeder may have difficulty in selecting the design best suited to achieve the described goals. Diallel analyses may be criticized (Gilbert, 1958; Baker, 1978), but they can still be of great benefit to the breeder and to the geneticist.

Griffing (1956b) proposed a diallel technique for determining the combining ability of lines and characterizing the nature and extent of gene action in both plants and animals. His approach has also been adapted to assess competition (e.g., Ames-Gottfred and Christie, 1989). Since its formulation, Griffing's analysis has been widely used by plant breeders (Buiatti *et al.*, 1974; Gomaa Gibrel *et al.*, 1982; Williams and Windham, 1988;

Krueger *et al.*, 1989). Wright (1985) describes the three levels of the analysis, and discusses the required assumptions at each level. Griffing's analysis allows the option to test fixed (model 1) or random (model 2) models.

As has been proposed by Griffing (1956a), the variance and covariance can be estimated by equating the expected to the observed mean squares or mean cross products. Also the population additive genetic and nonadditive genetic variances can be estimated from the combining ability components.

Griffing (1956b) proposed four methods of diallel crossing:

1. Method 1 (full diallel): The parents, F_1 and reciprocals included (p^2 total entries, where p is the number of parents).
2. Method 2 (half diallel): Parents and F_1's included but no reciprocals [p(p+1)/2 total entries].
3. Method 3: F_1's and reciprocals included, but no parents (p^2 - p total entries).
4. Method 4: F_1's included, but no reciprocals or parents [p(p-1)/2 total entries].

Griffing's analysis of combining ability requires no genetic assumptions (Wright, 1985) and has been shown to convey reliable information on combining potential of parents (Gill *et al.*, 1977; Bhullar *et al.*, 1979; Nienhuis and Singh, 1986).

Despite the appeal of Griffing's analysis, it is subject to several criticisms (Christie and Shattuck, 1992). In open-pollinated populations when the general combining ability (GCA) is the only parameter of interest, other designs such as the testcross, which are

less demanding of space and labor, have been suggested over this analysis (Baker, 1978). General combining ability of a genotype refers to its average performance in various cross combinations. Jenkins (1940) proposed a procedure for developing high yielding synthetic varieties which has come to be known as recurrent selection for general combining ability. It has been used extensively for population improvement and positive results have been reported (Lonnquist, 1949, 1951, and 1961; McGill and Lonnquist, 1955; Horner *et al.*, 1963; Penny, 1968).

Many studies using Griffing's analysis have shown that the performances per se of the parents are often associated with their combining abilities, i.e., promising parental performers tend to perpetuate desirable progeny (Gill *et al.*, 1977; Kumar and Agrawal, 1981; Mather and Poysa, 1983). This has prompted some researchers to question the predictive usefulness of the analysis. However, Gilbert (1958) discusses this aspect and relates the importance of diallels in uncovering unpredictable impotency or potency of parents which are not discernible in the performance of the parents themselves. It is possible that the favored direction of the expression of a character is due to complex interactions among genes that may be expressed recessively in certain genetic backgrounds and dominantly in others. This will influence the direction of F_1 expression when parents of different genetic backgrounds are crossed (Singh and Gupta, 1970). Furthermore, epistatic gene action may result upon hybridization, thereby causing unpredictable F_1 performance (Dick and Shattuck, 1990). The term specific combining ability (SCA) refers to the cases in which certain hybrid combinations perform relatively better or worse than expected on the basis of average performance of the parents

(Sprague and Tatum, 1942). When either dominance or epistasis occurs, the GCA and SCA effects of parents and crosses become evident only after conducting the diallel analysis (Christie and Shattuck, 1992).

Several studies (Matzinger *et al.*, 1959; Hayes and Paroda, 1974) have shown that GCA and SCA can interact significantly with the environment. Patil and Chopde (1981) and Soh *et al.* (1984) concluded that the analysis should be conducted in more than one environment in order to obtain reliable estimates for GCA effects.

There has been little discussion about the numbers of parents that should be included in a diallel despite it's obvious importance. Failure of assumptions (Nasser, 1965) and over- and under-estimation of genetic components may result when a limited number of parents are sampled. Hayman (1960) suggested that a minimum of 10 parents is necessary to estimate population parameters.

The Hayman and Jinks analysis has been used with species that are self-pollinated, or with those in which pure lines can be derived readily. The various analyses proposed by Griffing (1956b) can be used with any level of heterozygosity and polyploidy (Christie and Shattuck, 1992).

Gardner and Eberhart (1966) proposed an analysis for a diallel, in which each parent may be a random mating population, such as an open-pollinated pearl millet variety or maize cultivar. Each parent is assumed to be in Hardy-Weinberg equilibrium, with two alleles per locus. As will be seen, the analyses proposed by Gardner and Eberhart (1966) are similar to those proposed by Hayman (1954a, 1957) and to Griffing method 2 (1956b). Among the numerous, different kinds of analyses that have been proposed

for the diallel cross, the nonorthogonal analysis (Analysis II) suggested by Gardner and Eberhart (1966) allows one to estimate heterosis effects from a fixed set of varieties when the parent populations and their crosses (without reciprocals) are included in the analysis. Partitioning of the entry sum of squares is obtained by least square analysis and involves the use of a computer to invert several matrices that are needed to calculate the sums of squares.

Previous studies designed to obtain genetic and breeding information from a set of open-pollinated varieties of maize generally involved only the varieties and all possible crosses among them (Gardner and Paterniani 1967). From such tests, heterosis is estimated as the difference between the F_1 cross and the mean of the two parents:

$$\text{Heterosis} = F_1 - [(P_1 + P_2)/2].$$

In an effort to estimate heterosis more precisely and to estimate inbreeding depression and other useful genetic parameters, Gardner and Eberhart (1966) and Eberhart and Gardner (1966) extended the ideas developed by Robinson and Cockerham (1961) for two varieties and their descendants and by Hayman (1954a, 1954b, 1957, 1958, 1960) for a set of homozygous lines and their descendants. They formulated in detail expectations for the means of a fixed set of open-pollinated varieties, their F_1 crosses and other specified crosses that can be produced. The results obtained indicate that considerable genetic information can be obtained from an analysis of population means. At least some information in terms of gene effects and genetic variation can be obtained, and the genetic parameters that can be estimated have been found extremely useful for prediction purposes. Gardner and Paterniani (1967) believed

the most efficient and economical way to evaluate a number of varieties and races as to their breeding potential is to develop the needed populations and estimate means in a well designed and executed experiment.

For their statistical genetic model, Gardner and Eberhart (1966) considered the j^{th} random-mating variety with two alleles per locus and in Hardy-Weinberg equilibrium. Table 1 lists the genotypes, their frequencies and genotypic values for the i^{th} locus. 'A' represents the more favorable of the two alleles and 'a' the less favorable. Either could be dominant over the other, but in most studies, the more favorable allele has been found to be dominant. The mean of the two homozygotes is μ'. Additive gene action is indicated by α and the difference between the two homozygotes is 2α. The departure of the heterozygote from μ' due to dominance is indicated by σ.

Table 1. Genotypes, their frequencies and genotypic values for the i^{th} locus in the j^{th} random-mating variety with two alleles per locus assuming Hardy-Weinberg equilibrium.

Frequency	Genotype	Genotypic value
p^2_{ji}	AA	$\mu' + \alpha_i$
$2p_{ji}(1 - p_{ji})$	Aa	$\mu' + \sigma_i$
$(1 - p_{ji})^2$	aa	$\mu' - \alpha_i$

The means of the varieties (V_j), varieties selfed (V^s_j), variety crosses ($C_{jj'}$), variety crosses selfed ($C^s_{jj'}$), and variety crosses random mated ($C^r_{jj'}$) can then be expressed as follows:

$$V_j = \mu + a_j + d_j$$

$$V^s_j = \mu + a_j + \tfrac{1}{2}d_j$$

$$C_{jj'} = \mu + \tfrac{1}{2}(a_j + a_{j'}) + \tfrac{1}{2}(d_j + d_{j'}) + h_{jj'}$$

$$C^s_{jj'} = \mu + \tfrac{1}{2}(a_j + a_{j'}) + \tfrac{1}{4}(d_j + d_{j'}) + \tfrac{1}{2}h_{jj'}$$

$$C^r_{jj'} = \mu + \tfrac{1}{2}(a_j + a_{j'}) + \tfrac{1}{2}(d_j + d_{j'}) + \tfrac{1}{2}h_{jj'}.$$

where μ is the mean of random inbred lines for all varieties, $\mu + a_j$ is the mean of random inbred lines from the jth variety, and $\mu + a_j + d_j$ is the mean of the jth variety. The 'a_j' and 'd_j' represent the contributions of homozygous loci, and of heterozygous loci, to the jth variety mean. The $h_{jj'}$ are heterosis parameters that are due to differences in gene frequencies in varieties j and j' and due to dominance. They are expressed when varieties j and j' are crossed.

Gardner and Eberhart (1966) pointed out that when four or more parents are used to produce the diallel cross and related populations, the parameter $h_{jj'}$ can be partitioned to provide additional information as, $h_{jj'} = \bar{h} + h_j + h_{j'} + s_{jj'}$,

Where $\bar{h}$ is the average heterosis contributed by the particular set of varieties used in crosses; h_j is the average heterosis contributed by variety j in its crosses measured as a deviation from average heterosis ($\Sigma_j h_j = 0$), $h_{j'}$ is the average heterosis contributed by variety j' in its crosses, and $s_{jj'}$ is the specific heterosis that occurs when variety j is mated to variety j'. The restriction $\Sigma_j s_{jj'} = 0$ is required.

Gardner and Eberhart (1966) proposed three types of analysis for diallel cross as follows:

Analysis I:

When n varieties ($n \geq 4$) and the 5 kinds of populations suggested by Gardner and Eberhart (1966) are available, all the parameters defined above in genetic terms can be estimated by the method of least squares and the heterosis constants can be further subdivided as indicated to provide additional information about the parental varieties involved. The estimates obtained are particularly useful in making predictions (even about populations not included in the experiment) and in choosing breeding material and breeding systems. They also provide information on inbreeding depression, heterosis, additive gene action, dominance, and epistasis (the latter indicated by lack of fit of the model when a sufficient number of entries are included in the experiment). By utilizing a modern computer, one can easily estimate the constants, and by fitting successively more complicated models, one can draw conclusions about the statistical significance of the different kinds of parameters in the model. Let $(B'G)_i$ ($i = 1, 2, ..., 5$) be the sum of squares due to fitting the above defined constants in the ith model below, as suggested by Eberhart (1964) and Gardner and Eberhart (1966):

Model	Constant included	Sum of squares
1	μ, a_j	$(B'G)_1$
2	μ, a_j, d_j	$(B'G)_2$
3	μ, a_j, d_j, $\bar{h}$	$(B'G)_3$
4	μ, a_j, d_j, $\bar{h}$, h_j	$(B'G)_4$
5	μ, a_j, d_j, $\bar{h}$, h_j, s_{ij}	$(B'G)_5$

To estimate all of the above parameters, five generations are needed:

(1) parents,

(2) parent self-pollinated,

(3) F_1 crosses,

(4) F_1 self-pollinated, and

(5) F_1 crosses random mated.

The total sum of squares for population means would be subdivided as in Table 2 (Analysis I) as suggested by Gardner and Eberhart (1966).

Table 2. The sum of squares for population means for Analysis I.

Source	d.f.	Sum of Squares
Populations	$[n(3n + 1)/2] - 1$	S
a_j	$n - 1$	$S_1 = (B'G)_1 - CF$
d_j	n	$S_2 = (B'G)_2 - (B'G)_1$
$h_{jj'}$	$n(n - 1)/2$	$S_3 = (B'G)_5 - (B'G)_2$
$\bar{h}$	1	$S_{31} = (B'G)_3 - (B'G)_2$
h_j	$n - 1$	$S_{32} = (B'G)_4 - (B'G)_3$
$s_{jj'}$	$n(n - 3)/2$	$S_{33} = (B'G)_5 - (B'G)_4$
Residual	$n(n - 1)$	$S_4 = S - S_1 - S_2 - S_3$

n is the number of parents in the diallel

Analysis II:

The addition of the varieties to the variety cross diallel permits the separation of all heterosis effects using the following model, assuming no epistasis. When only the parent varieties and their n(n - 1) crosses are grown in the experiment, a_j and d_j are confounded and must be estimated jointly. Gardner and Eberhart (1966) defined the following additional parameters in relation to those already defined:

μ_v = the mean of all parental varieties included

$= \mu + \Sigma_j\, d_j/n = \mu + \bar{d}$,

$V_j = a_j + (d_j - \bar{d})$

= the variety effect when parental varieties are included in the analysis.

As before, let $(B''G)_i$ (1, 2, ..., 4), be the sum of squares due to fitting the constants included in the following models:

Model	Constants included	Sum of Squares
1. $Y_{jj'} = \mu_v + \frac{1}{2}(V_j + V_{j'})$	μ_v, V_j	$(B''G)_1$
2. $Y_{jj'} = \mu_v + \frac{1}{2}(V_j + V_{j'}) + k\bar{h}$	μ_v, V_j, $\bar{h}$	$(B''G)_2$
3. $Y_{jj'} = \mu_v + \frac{1}{2}(V_j + V_{j'}) + k\bar{h} + k(h_j + h_{j'})$	μ_v, V_j, $\bar{h}$, h_j	$(B''G)_3$
4. $Y_{jj'} = \mu_v + \frac{1}{2}(V_j + V_{j'}) + k\bar{h} + k(h_j + h_{j'}) + ks_{jj'}$	μ_v, V_j, $\bar{h}$, h_j, $s_{jj'}$	$(B''G)_4$

In these models

$k = 0$ if $j = j'$

$= 1$ if $j \neq j'$,

In this analysis the a and d components can not be separated so the researcher estimates parameters, such as V_j and $h_{jj'} = \bar{h} + h_j + h_{j'} + s_{jj'}$ (Table 3), which have no direct genetic

interpretation (Christie and Shattuck 1992). It should be noted, however, that the V_j and h_j components can be calculated for each parent, and the $s_{jj'}$ component for each combination. Singh (1978) and Ordas (1980) give details of the necessary calculations, and the paper by Misevic *et al.* (1989) is an example of the use and interpretation of the parameters.

Table 3. The sum of squares for population means for Analysis II.

Source	d.f.	Sum of Squares
Populations	$[n(n+1)/2]-1$	S'
Variety (V_j)	n-1	$S'_1 = (B'G)_1 - CF$
Heterosis ($h_{jj'}$)	$n(n-1)/2$	$S'_2 = (B'G)_4 - (B'G)_1$
Average ($\bar{h}$)	1	$S'_{21} = (B'G)_2 - (B'G)_1$
Variety (h_j)	n-1	$S'_{22} = (B'G)_3 - (B'G)_2$
Specific ($s_{jj'}$)	$n(n-3)/2$	$S'_{23} = (B'G)_4 - (B'G)_3$

n is the number of parents in the diallel

The inbreeding effects (d_j) still can not be separated from a_j unless the varieties selfed and/or the variety crosses selfed are included. When the design includes varieties (Y_j), all possible variety crosses ($Y_{jj'}$), varieties selfed (Y^s_j), and/or variety crosses selfed ($Y^s_{jj'}$), the following models can be used and all parameters except additive by additive epistasis can be estimated (Gardner and Eberhart, 1966; Eberhart and Gardner, 1966; Gardner and Paterniani, 1967):

$$Y_{jj'} = \mu + \tfrac{1}{2}(a_j + a_{j'}) + \tfrac{1}{2}(d_j + d_{j'}) + k\bar{h} + k(h_j + h_{j'}) + ks_{jj'}$$

$$Y^s_{jj'} = \mu + \tfrac{1}{2}(a_j + a_{j'}) + \tfrac{1}{4}(d_j + d_{j'}) + \tfrac{1}{2}k\bar{h} + \tfrac{1}{2}k(h_j + h_{j'}) + \tfrac{1}{2}ks_{jj'}$$

where

$Y_{jj'}$ is the mean of the cross between variety j and variety j',

$Y^s_{jj'}$ is the predicted mean of the selfed cross of varieties j and j'.

Gardner and Eberhart (1966) showed that unless populations produced by selfing the varieties and/or the variety crosses are grown, the μ, a_j, and d_j parameters cannot be estimated separately. The separation of a_j and d_j provides information on the cumulative contribution of homozygous and heterozygous loci to variety means and permits a more precise understanding of inbreeding depression as indicated by the above equations. The $h_{jj'}$ and its subdivision provide information on heterosis, and the residual due to deviations from the model in the analysis of variance provides information on epistasis and linkage.

A diallel that includes parents plus the F_1s can be analyzed using Griffing's Method 2 (1956b). In this case, if the parents are random mating populations, model 1 can be

used and estimates derived for general specific combining ability. Gardner and Eberhart (1966) have some criticism of that analysis. The mean square for specific combining ability is taken as a measure of nonadditive genetic effects. Gardner and Eberhart (1966) have pointed out that the mean square for varieties vs. crosses, or average heterosis, is also a measure of nonadditive genetic effects. Therefore, Griffing's (1956b) Method 2, Model 1 does not indicate clearly the level of heterosis and the genetic effects involved. Gardner and Eberhart (1966) considered Analysis II to be the best analysis available for a diallel involving populations as parents, but considered their Analysis III superior to Griffing's (1956b) Method 2, Model I.

Table 4. The analysis of variance for Analysis III has the following form for n parents.

Source	d.f.	Sum of Squares
Populations	[n(n + 1)/2] - 1	S''
Cultivars	n - 1	S''_1
Cultivars vs Crosses	1	S''_2
Crosses	[n(n - 1)/2] - 1	S''_3
GCA (g_j)	n - 1	S''_{31}
SCA ($s_{jj'}$)	n(n - 3)/2	S''_{32}

n is the number of parents in the diallel.

Analysis III:

Eberhart and Gardner (1966) stated that when the diallel includes variety crosses only, no tests for epistatic effects are available and the usual model

$Y_{jj'} = m + g_j + g_{j'} + s_{jj'}$

(where $Y_{ij'}$ is the mean of the cross between variety j and variety j') is the best model available. Additive by additive epistatic effects are confounded with both the general combining ability (g_j) and specific combining ability ($s_{jj'}$) effects if they are of importance. The average heterosis is confounded with the mean and the variety heterosis is confounded with the general combining ability effect (g_j). If epistasis is negligible the relation of parameters is as follows:

$$m = \mu + \bar{d} + \bar{h}$$

$$g_j = \tfrac{1}{2}[a_j + (d_j - \bar{d})] + h_j$$

$$s_{jj'} = s_{ij'}$$

where $\bar{d} = 1/n \, \Sigma \, d_j$.

$Y_{jj} = \mu_v + V_j$ for the parents, and

$Y_{jj'} = \mu_c + g_j + g_{j'} + s_{jj'}$ for the crosses,

where g_j = general combining ability of parent j,

and $s_{jj'}$ = specific interaction between parent j and parent j'.

In relation to Analysis II:

$m = \mu_c = \mu_v + \bar{h}$

μ_c = mean of all crosses

and

$g_j = \frac{1}{2}V_j + h_j$ so

$Y_{jj'} = \mu_c + g_j + g_{j'} + s_{jj'} = \mu_v + \frac{1}{2}(V_j + V_{j'}) + k\bar{h} + k(h_j + h_{j'}) + ks_{jj'}$

where k = 0 when j = j' and 1 when $j \neq j'$

The mean square for $s_{jj'}$ will be the same in both analyses (Analysis II and III), and the mean square for the average heterosis (Analysis II) will be equal to the mean square for cultivars vs. crosses (Analysis III) (Tables 3 and 4). In the analysis provided by Griffing (1956b) the d.f. for SCA is given by n(n-1)/2. In Analysis III, the effect of cultivar and cultivars vs. crosses has been removed from the mean square for SCA, along with n d.f. (Table 4). Estimation of V_j and g_j can be obtained for each parent and the $s_{jj'}$ for each combination. Gerrish (1983) used this analysis to evaluate exotic maize germplasm.

These three analyses (Analysis I, Analysis II, and Analysis III) are for fixed effects: that is, there is no base population. Although the models and analyses were developed for studies with random-mating varieties as parents, the gene frequencies are arbitrary. Consequently, as Gardner and Eberhart (1966) emphasized, the analyses can be used also where the parents are inbred lines and pure-line varieties.

The parameters estimated in Analysis II and III have no direct counterpart in genetics. "How one does utilize these estimates?" asked Christie and Shattuck (1992). From Analysis II, the values of V_j and h_j for each parent indicate the potential of that parent in crosses. Values of $s_{jj'}$, considered in relation to V_j and h_j, would indicate the best combination(s) of parents for hybrids. Hallauer and Eberhart (1966) found that specific heterosis effects ($s_{jj'}$) were negligible and concluded that selection could be based on

variety performance. The predicted means, $V_{jj} = \mu_v + V_j$ were considered the best estimates of parental potential. Troyer and Hallauer (1968), Dudley *et al.* (1977), and Mungoma and Pollak (1988) analyzed data using both Analysis II and III. Dudley *et al.* (1977) concluded that more information can be obtained from the two analyses than from either one of them alone. They reported that the mean squares for heterosis were the most valuable part of Analysis II, while the mean squares for parents and general combining ability from Analysis III were more valuable than parent mean square from Analysis II. Misevic *et al.* (1989) used Analysis II to estimate the V_j, h, h_j, and $s_{jj'}$ effects and also used Analysis III to estimate g_j effects.

Singh and Singh (1984) compared Analysis II and III with various other half-diallel designs. They concluded that Analysis II provided more information on heterosis than Analysis III, because Analysis II and III partition the sums of squares for heterosis into different components. Analysis II partition the entries sum of squares into variety (V_j) and heterosis ($h_{jj'}$) effects, and $h_{jj'}$ was further divided into average ($\bar{h}$), variety (h_j), and specific ($s_{jj'}$) heterosis (Table 3). Analysis III partition the entries sum of squares into cultivars, cultivars vs crosses, and crosses, and further divided the crosses into GCA (g_j) and SCA ($s_{jj'}$) effects (Table 4). Average heterosis in Analysis II is the same as cultivars vs crosses and specific heterosis (Analysis II) is the same as specific combining ability (Analysis III). The other three sources of variation in Analysis II and III are different.

Eberhart and Gardner (1966) extended the models and analyses by providing for the partitioning of direct heterosis effects and the estimation of additive by additive effects

with parents that have multiple alleles. These analyses have been used with many plant species (Eagles, 1982; Valladares-Sanchez *et al.*, 1983; Huen, 1987; Lamb *et al.*, 1987).

Results from maize

Pollak *et al.* (1957) considered open-pollinated varieties, their F_1, F_2 and backcross generations. Results from two locations in a single year gave no significant deviation from a linear relationship between performance and level of heterozygosity. Most maize varieties investigated in the United States have relatively large amounts of genetic variance and the additive genetic variance is generally higher than the nonadditive (Gardner, 1963; Lonnquist, 1949; Gardner and Paterniani, 1967).

Robinson and Cockerham (1961) developed a procedure for relating performance to level of heterozygosity utilizing two heterogenous parent populations of maize, their F_1 cross, F_2, and the selfs of each. They indicated that lack of a linear relationship would support the theory of epistatic gene action. They showed that the relationship between performance and heterozygosity was found to be essentially linear for both yield and ear height. They found that heterosis, measured from the midparent, was manifested in the cross for yield but not for ear height.

Moll *et al.* (1965) studied the relationship of heterosis and genetic divergence in maize. Their results indicated that heterosis increased with increased divergence within a restricted range of divergence, but extremely divergent crosses resulted in a decrease in heterosis.

The estimation of additive and nonadditive variation in maize varieties requires extensive experiments in order to give the kind of precision needed to differentiate between varieties (Gardner and Paterniani 1967). From results obtained by using six open-pollinated varieties of maize and their descendant progenies, they found that the variety effects and heterosis effects were both highly significant, indicating the existence of dominance and differences in gene frequencies among the varieties as well as differences in general combining ability. They also found that when partitioning heterosis, only average heterosis was statistically significant.

Crossa *et al.* (1990) studied heterotic patterns among Mexican races of maize, and their combined analysis of variance for 2 yr at high elevation for grain yield showed that 69% of the sum of squares among entries was attributed to variety effects (V_j) and 31% could be explained by heterosis effects ($h_{jj'}$). They found that specific heterosis ($s_{jj'}$) was the most important component of $h_{jj'}$. Similar results were found by Miranda and Vencovsky (1984) when studied nine open-pollinated varieties crossed in a diallel mating scheme.

Results from sorghum

Cheng *et al.* (1989) studied 100-grain weight in sorghum in a diallel crosses involving nine sets of male-sterile lines and their maintainers, showed that the 100-grain weight was controlled by 4 alleles that fit an additive-dominance model. Dominant genes, which were more frequent, increased grain weight and recessive genes decreased it. They found that the relative heritability was on average 1.83 for higher grain weight parents

(HGWP) and minus 0.83 for lower grain weight parents (LGWP). The contribution of the HGWP to F_1 grain weight was significantly higher than that of LGWP.

Lazanyi *et al.* (1983) revealed the importance of overdominance in leaf length, forage and grain yield of sorghum. They suggested that plant height was governed by 2-3 genes, leaf length by 3-4 genes, stalk mass by 2-3 genes, and grain mass by 3-4 genes. The largest heterosis effect was noticed between characters associated with grain yield and stalk yield. The highest additive gene effect was observed in the inheritance of stalk yield and leaf number based on V_{GCA}/V_{SCA} values (the ratio between GCA variance and SCA variance).

Patil and Thombre (1983) noted high heritability for vegetative and reproductive traits studied in sorghum, both in F_1 and F_2 generations of a 9 x 9 diallel cross.
Combining ability analysis revealed that sorghum varieties with good general combining ability would give better heterosis in their F_1 hybrids, and hence crosses between the best general combiners would produce high yielding genotypes in segregating generations like the F_2 and F_3 (Nandanwankar *et al.*, 1983).

Nagabasaiah (1982) studied performance per se, combining ability and gene action for ten quantitative characters in a complete diallel analysis of seven parents in sorghum for the F_2 generation. His analysis of variance showed highly significant differences among genotypes for all characters. He found that additive gene action was predominant for plant height, internode length, leaf breadth and panicle length, while nonadditive gene action was more important for leaf number, leaf length, and grain yield, but both were equally important for days to 50% flowering, panicle breadth and 1000-grain weight.

Results from pearl millet

Sharma *et al.* (1987a) analyzed the variance for combining abilities in a 12 x 12 diallel cross involving six open-pollinated varieties and six inbreds of pearl millet to show additive and nonadditive gene effects for green fodder yield and plant height. They found that results from these diallel crosses, one each for inbreds and open-pollinated populations, gave estimates of gene effects that varied considerably from those obtained from the 12 x 12 diallel cross involving both inbreds and varieties.

Sharma *et al.* (1987b) crossed 13 diverse pearl millet inbreds in a half-diallel design to evaluate combining ability for green fodder yield. Their analysis revealed that about 80% of the total variance in the diallel cross was due to specific combining ability (SCA), indicating a preponderance of nonadditive gene effects. The variance due to GCA represented only 2% of the total. When making line x tester crosses, the proportion of the total variance resulting from SCA effects varied from about 48 to more than 66%, depending on the GCA of the tester used, while the proportion resulting from GCA effects was not more than 20%; again, a preponderance of nonadditive gene effects was indicated. They concluded that combining ability and genetic diversity are interrelated.

Kushwah and Singh (1992) provided information on heterosis derived from data of 13 yield-related traits in the 66 crosses from 12 inbred lines in a diallel fashion (three each of Indian and African origin and six derived indigenous x exotic crosses) of pearl millet. Heterosis for grain yield ranged from 78% to 397%, and the derived lines were generally better than the indigenous and the exotic lines in the expression of heterosis.

Ouendeba *et al.* (1993) used five African land races of pearl millet in diallel crosses. They measured plant height, flowering time, natural incidence of downy mildew (*Sclerospora graminicola*), panicle length, grain yield, and 1000-seed mass in different populations. Six out of the ten crosses showed significant heterosis and gave 36 to 81% more grain yield than their better parents. Mean squares for GCA were significant for most traits indicating the importance of additive gene effects for these traits. The large heterotic effects and the magnitude of the additive effects, should be useful in choosing pearl millet landraces for intercrossing in the development of cultivars with improved grain yield.

Muza (1990) studied combining ability and stability of grain yield of pearl millet in four states at six sites in the United States in 1988. The entries included consisted of three open-pollinated populations, three topcross (TC) and three single-cross (SC) hybrids and their parents. A predominance of additive gene action was indicated and hence, recurrent selection should be useful for breeding high yielding open-pollinated varieties.

Talukdar *et al.* (1993) evaluated the time to 50% flowering for seven pearl millet inbreds with good GCA for grain yield and their 21 F_1 hybrids under normal and extended day lengths. For ICMP 83401 and ICMP 451, GCA effects for time to 50% flowering were significant and negative under both summer normal day length (SNDL) and summer extended day length (SEDL). The GCA estimates for photoperiod sensitivity for these two parents were also significant and negative. Their results indicated the usefulness of these two parents for generating early flowering photoperiod-insensitive progenies.

The literature on pearl millet reveals there is a large amount of variability for a number of traits and that a great proportion of this variability is thought to be additive in nature. The diallel mating design provides information on the breeding potential of the parents which can not be otherwise known from their phenotypic performances. Use of the variety diallel cross Analysis II is particularly useful in predicting the heterosis and variety effects, and hence the type of genetic effects involved in the expression of different traits.

Among the major constraints to increasing yields for subsistence farmers in both India and Africa, is the low genetic potential of local landraces. Pearl millet breeding began in both India and Africa with emphasis on grain production. Initially, open-pollinated local landraces were improved by mass selection. Later, several commercial hybrids were produced in India, however, they are less widely adopted by farmers in harsher environments, often being more susceptible to diseases, less well adapted to abiotic stresses than locals, resulting in unstable yield performance (Anand Kumar,1989; Hash, 1994). The development of superior genotypes depends largely on the frequency of favorable alleles and gene combinations in the populations from which they are derived. In predominantly cross-pollinated crops such as maize and pearl millet, recurrent selection has been shown to be an effective breeding method for accumulating favorable alleles at a large number of loci, and in providing repeated opportunities for favorable gene combinations to develop without undue compromise on the magnitude of genetic variability (Allard, 1960; Andrews *et al.*, 1977). With overdominance and epistasis being small in magnitude and rather infrequent in occurrence, recurrent selection for general

combining ability has been suggested as the most suitable approach to population improvement (Moll and Stuber, 1974). Therefore, information on different varieties and composite populations are very important for the breeding programs aiming at developing open-pollinated varieties or parents of hybrids.

To develop composite base populations for future recurrent selection programs, a diallel cross of eleven pearl millet populations was produced to combine high yield performance of elite populations with other desirable traits to achieve the objectives outlined for this study. The analyses can be carried out using Analysis II suggested by Gardner and Eberhart (1966) for the variety diallel cross and parents excluding reciprocals to provide information on variety and heterosis effects. This information can be used to indicate the additive and nonadditive genetic effects of prospective parents, which would enable us to develop one or two populations having high mean yield and desirable agronomic traits, and identify appropriate breeding methods for their future improvement. These populations can be used to generate open-pollinated cultivars suitable for the semi-arid tropics of India and Africa. Alternatively, two or more populations can be developed for generating inbred parents of hybrids in future.

Materials and Methods

MATERIALS AND METHODS

Development of genetic material

A diallel set of crosses was produced Dr C Tom Hash and Mr AG Bhaskar Raj, in pearl millet breeding section of the Genetic Enhancement Division at ICRISAT Asia Center (IAC) among 11 populations of pearl millet in the dry season of 1993. The parental populations were chosen on the basis of their performance in grain yield, panicle characteristics, vegetative growth rate, resistance to diseases (mainly downy mildew caused by *Sclerospora graminicola* (Sacc.) J. Schröt., smut caused by *Tolyposporium penicilliariae* Bref., and ergot caused by *Claviceps fusiformis* Loveless), and medium to late maturity for Indian conditions. The eleven populations included in this diallel were:

(i) **ICMV 155**: This is a variety developed at IAC by random mating 59 mass-selected selfed plants from the C_4 cycle of the ICRISAT New Elite Composite (NELC). It is thick stemmed, of medium maturity, resistant to downy mildew, and was released in India as an open-pollinated variety in 1991 (Pheru Singh *et al.*, 1994).

(ii) **ICMP 87307**: This is the seventh cycle random-mated bulk of the ICRISAT Inter Varietal Composite (IVC). It is a full season, tall, dual-purpose/grain population with long compact, cylindrical panicles and medium grain size.

(Open-pollinated variety Raj 171, released in Rajasthan in 1990 as a higher-yielding replacement for WC-C75, was bred from an earlier cycle of this composite).

(iii) **ICMP 91751**: This is the first cycle random-mated bulk of the ICRISAT Smut Resistance Composite II (SRC II). It is tall, of medium long duration, with long medium-compact panicles. It has very high grain yield potential for a dual purpose/grain population. It has good levels of resistance to downy mildew and smut.

(iv) **ICMP 87200**: This is the initial cycle random-mated bulk of the ICRISAT Ergot Resistant Composite (ERC). It is tall, and of long duration with long panicles. It is resistant to downy mildew, smut and ergot.

(v) **NWC C2**: This is the second cycle random-mated bulk of the Nigerian World Composite. It is a tall, dual purpose/grain population of medium-long duration.

(vi) **AfPop 88**: This feeder population was developed by random mating inbred bulks selected at IAC out of breeding material received from different stations in western and central Africa.

(vii) **AfPop 90**: This feeder population was developed by random mating selfed inbred bulks selected at IAC out of breeding material from Zimbabwe (NARS and ICRISAT) and Zambia (NARS).

(viii) **ICMP 92591**: This is the first cycle random-mated bulk of Lubasi (late backup synthetic). It is a tall, long-duration, dual purpose/grain population with long cylindrical panicles and high grain yield potential. Lubasi was obtained from the

Zambian national program, but is based largely on later maturing breeding materials from IAC.

(ix) **LHGP**: The Large Headed Genepool from the Genetic Resources Division at IAC is a tall, long duration population with large panicles. It was developed by 4 cycles of random mating of 804 germplasm accessions selected on the basis of their large panicles (length >55 cm and thickness >35 mm).

(x) **SenPop**: This is the initial cycle bulk of an IAC feeder population developed by backcrossing and selection involving a weedy accession from Senegal and the F_1 of the cross ICMV 87901 x ICMV 82132. ICMV 87901 was bred from the third cycle of the ICRISAT Bold Seeded Early Composite. ICMV 82132 was bred from the ICRISAT Smut Resistant Composite. SenPop is of long duration, and has both a high vegetative growth rate and a high grain yield potential.

(xi) **ICMV 91059**: This variety was developed by random mating 42 selected non-bristled S_1 progenies from ICMS 8359, a highly variable synthetic variety having high yield potential. This synthetic was developed by random mating a set of pedigree-derived inbred lines and hence was distantly related to the other elite parents (i - iii) in this diallel.

The 11 parents were mated at IAC during the dry season in 1993, following a diallel plan without reciprocals. Matings between each pair of the open-pollinated parents were produced by full-sib crosses between at least 40 to 50 plants of each parent in each

mating. A plant was used in a mating only once as either a female or a male. At maturity, the seed-parent panicle of each full-sib progeny within a mating was cut, sun-dried, and threshed separately. Next, samples of seed from each full-sib progeny within a mating were composited, and this composite subsequently represented the mating between these two open-pollinated parents. The parents (10 parents only, because one is very late to flower) and F_1 mating composites were selfed in the 1994 dry season to produce selfed progenies. The self-pollinated generation of the parent populations and the F_1 matings were each produced by self pollinating at least 60 to 80 plants. At maturity, each selfed plant from the parent population or F_1 mating was harvested, sun-dried, and threshed separately. Next, samples of seed from all selfed panicles for each selfed generation were composited. These composites were the sources of seed for the evaluation experiment. Thus, seed lots of the parents and the F_1 were produced in the same dry season (1993) in the same field, and the selfed generations were produced in the next dry season (1994) in the same field.

Field evaluation

Evaluation of the various populations were conducted in field experiments during the rainy season of 1993 at two locations in India, Bhavanisagar (11°N) and Patancheru (17°N), and in summer 1994 (January to April) in Patancheru by millet breeding section (C Tom Hash). These experiments included parents, F_1 hybrids, and six control entries (72 total entries). During the 1994 and 1995 rainy seasons (June - October), field experiments were conducted in Patancheru only, with a total of 144 entries (parents, F_1

hybrids, selfed progenies of both the parents and the F_1s, and 13 controls). In 1995 rainy season I repeat this experiment in Patancheru and the previous seasons were included in this study for M.Sc. degree. All five experiments contained 66 common experimental entries representing the 11 parents and the F_1 hybrids of their 55 matings, and six common controls (total 72 entries). The 1994 and 1995 rainy season field experiments included the above 72 entries plus 10 selfed parents (all except LHGP which flowered too late to mature seed in the 1994 summer nursery), the selfed F_1 hybrids of all 55 matings, and seven more controls (total 144 entries). The six common controls were NELC C7, NELC C8, IVC C8, SRC II C2, MC C10, and WC-C75. The additional controls used during the 1994 and 1995 rainy seasons were ICMV 155, NELC C8, IVC C8, SRC II C2, MC C10, WC-C75, and ICMH 451.

The experiments were conducted in randomized complete block designs with three replications on Alfisol soil at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, at 17°N latitude. Rainfall in Patancheru was 505 mm during the 1993 rainy season, 18 mm during 1994 dry season, 448 mm during the 1994 rainy season, and 684 mm during the 1995 rainy season. Furrow irrigation was used throughout the 1994 dry season sowing at Patancheru, while flood irrigation was used in the 1993 Bhavanisagar sowing because the amount of precipitation was not sufficient. The plot consisted of four 5 m rows spaced 75 cm apart. At Patancheru the experiments received 40 kg N ha^{-1} and 40 kg P ha^{-1} as a basal application and 40 kg N ha^{-1} at 20 to 30 days after emergence. The Bhavanisagar experiment received 45 kg N, 45 kg P, and 45 kg K ha^{-1} as a basal application and 45 kg N ha^{-1} three weeks after

sowing. Patancheru sowing dates were 2 July in 1993, 23 June in 1994, and 19 June 1995 for the rainy season experiments, and 10 January in 1994 for the summer season experiment. The Bhavanisagar experiment was sown on 9 June 1993. Two weeks after emergence, seedlings were thinned to one plant per 15 cm of row (120 000 plants ha^{-1}). Plant counts were taken from the two central rows after thinning to determine the actual plant population. Flowering date and plant height were assessed on a whole plot basis (Table 5). At maturity, panicles of plants in the two central rows of a plot (7.5 m^2) were cut, counted, oven dried at 65°C or sun dried, weighed, threshed, and their grain weighed to determine grain yield per plot. Next, stover from the two central harvested rows was cut and weighed. A sample of the stover was chopped, weighed, and dried at 65°C, and dry matter yield at maturity was determined. A grain sample was taken from each plot in 1995 for 1000-seed mass determinations.

Traits

Traits measured on parents and their progenies, their abbreviations, and methods of measurements are presented in Table 5. All traits were measured on all three replications. Growth index (GI) was calculated using the procedure proposed by Bramel-Cox *et al.* (1984). All traits were measured at harvest except for time to flowering (TFL), which was recorded at flowering, plant count two to three weeks after thinning, and plant height and panicle length which were measured two weeks before harvest. Dry weights were recorded from plant materials dried for 24 h at 65°C.

Statistical analysis

All statistical analyses were performed using the software package Genstat version 4 from Rothamstead Experimental Station. Analyses of variance were performed on the data from individual environments and then combined across environments when error variances were homogeneous. Randomized block design (RBD) analysis was used to determine entry mean differences among the 66 common experimental entries.

Genetic model

The genetic model for a fixed set of diploid open-pollinated varieties of a cross-pollinated species is based on the assumption that the parent populations are in Hardy-Weinberg equilibrium with respect to a single locus and in linkage equilibrium with respect to any pair of loci. Many authors believe that open-pollinated varieties of cross-pollinated crops meet these assumptions reasonably well, although others disagree. The genetic information on the populations was obtained using model II suggested by Gardner and Eberhart (1966). The model II analysis was based on fitting the variety and variety cross means to the linear model:

$$Y_{ij} = \mu_v + \tfrac{1}{2}(V_i + V_j) + k(\bar{h} + h_i + h_j + s_{ij}),$$

where

Y_{ij} is the mean of the cross between i^{th} and j^{th} parents;

μ_v is the mean of all varieties;

V_i and V_j are the variety effects for variety i and variety j;

$\bar{h}$ is the average heterosis contributed by all varieties used in crosses;

h_i and h_j are the contribution of each variety to the expression of heterosis; and s_{ij} is the specific heterosis that occurs when variety i is mated to variety j;

k = 0 when i = j and,

= 1 when i $\neq$ j.

A fixed model was used. Variety effects (V_i) represent part of the additive gene effects and can be described as the difference between the mean of a parent per se and the mean of all parents (Gardner, 1967). In this study the term heterosis effects (h_{ij}) are related to nonadditive gene effects and were defined as $h_{ij} = \bar{h} + h_i + h_j + s_{ij}$ (Hayman, 1954a), where $\bar{h}$ is the average heterosis, h_i is the deviation from $\bar{h}$ contributed by variety i in its crosses, and s_{ij} is the specific heterosis for the cross ij. The formula used for determining variety heterosis (h_i) was as defined by Gardner (1967):

$$h_i = \{[(n - 1)/(n - 2)](Y_i - Y_c)\} - [\tfrac{1}{2}(Y_{ii} - Y_v)]$$

where n is the number of parents, Y_i is the mean of variety i in crosses, Y_c is the mean of all crosses, Y_{ii} is the mean of variety i per se, and Y_v is the mean of all varieties per se.

Environmental effects were considered to be random, and genotypes x environment interaction was used for testing significance. The standard errors (SE) for the different estimates were calculated as follows, according to Singh (1978)):

$$SE(\mu_v) = \{2MSE/n(n + 1)\}^{1/2}$$

$$SE(V_i) = [MSE(n - 1)/n]^{1/2}$$

$$SE(h) = \{[MSE(n + 1)]/n(n - 1)\}^{1/2}$$

$SE(h_i) = \{[MSE(n - 1)(n + 2)]/4n(n - 2)\}^{½}$

$SE(s_{ij}) = \{MSE(n - 3)/(n - 1)\}^{½}$ for $(i \neq j)$

F-tests were used to determine significance of mean squares due to differences among main effects, interactions, and genetic parameters by using the entry x environment mean square (Steel and Torrie, 1960; Crossa *et al.*, 1987). When the entry x environment effect was nonsignificant, this source of variation was pooled with the error mean square. The degrees of freedom associated with this pooled error were the sum of degrees of freedom for error and entry x environment interaction. This pooled error was used to make all tests of significance. When the degrees of freedom are big enough there is no need for pooling as in our case and we just use the error mean square for testing significance when interaction effect is nonsignificant. One degree of freedom was subtracted from the error term for each missing value.

The genetic parameters that contribute significantly to a trait and the sums of squares associated with each genetic parameter are determined by successively fitting more complex models to the data via least squares method. The mean squares due to fitting each genetic parameter are 1) tested for significance and 2) compared with the generations sum of squares for a trait.

The mean of the parents and their n(n-1)/2 crosses and the selfed progenies from the parents and selfed progenies from their crosses can be expressed in terms of genetic parameters defined by Eberhart and Gardner (1966) and Gardner and Paterniani (1967)

and the generation means for a trait (Y) is written as a function of the cumulative additive (a), dominance (d) and heterosis (h) and additive x additive (aa) genetic effects.

Variety mean:

$$Y_i = \mu + a_i + d_i$$

F_1 cross mean:

$$Y_{ij} = \mu + \tfrac{1}{2}(a_i + d_i) + \tfrac{1}{2}(a_j + d_j) + h_{ij} + aa_{ij}$$

where

Y_i is the mean of the parent i,

Y_{ij} is the cross mean of the i^{th} and j^{th} parent,

a_i and a_j are the cumulative additive effects for parents i and j, respectively,

d_i and d_j are the cumulative dominance genetic effects for parents i and j, respectively,

h_{ij} is the heterosis effects from the cross of parents i and j, and

aa_{ij} is the additive x additive epistatic effects from the cross of parents i and j.

μ is the mean of random homozygous lines that could be developed from the varieties in the set of diallel, $\mu + a_i$ is the mean of random homozygous lines that could be developed from the variety i, d_i is a function of heterozygous loci in the ith variety and is involved in inbreeding, aa_{ij} is a function of inter-variety additive x additive epistasis, arises as a consequences of differences in gene frequencies in the two varieties when non-alleles interact with one another.

The selfed progenies from the varieties and from the F_1 crosses have been included in the 1994 and 1995 rainy season experiments at Patancheru. Therefore, their means

would have the following expectations:

Variety selfed mean:

$$Y^{s}_{i} = \mu + a_i + \tfrac{1}{2}d_i$$

F_1 cross selfed mean:

$$Y^{s}_{ij} = \mu + \tfrac{1}{2}(a_i + a_j) + \tfrac{1}{4}(d_i + d_j) + \tfrac{1}{2}h_{ij} + aa_{ij}$$

The variety effects (V_i) can be calculated as the difference between the mean of variety i and the mean of all varieties, i.e.

$V_i = Y_i - \mu_v$, for each variety,

whereas general combining ability (g_i) can be calculated by

$g_i = \tfrac{1}{2}(V_i) + h_i$, for each variety.

For the purpose of this degree, only parents and F_1 hybrids are included in the analysis by using Analysis II proposed by Gardner and Eberhart (1966) for the variety diallel cross to estimate genetic constants and mean performance of the parents and crosses involved in the diallel.

Table 5. Traits measured on pearl millet diallel populations and progenies derived from them, and their abbreviations, and methods of measurement or calculation.

Traits	Abbrev-iations	Methods of measurements or calculations
Time to flowering	TFL	days after emergence when 75% of plants in the plot had panicles with emerging stigmas (DAE)
Panicle yield	PYD	mass of panicles from 5 m length of two rows (g/7.5 m^2)
Grain yield	GYD	mass of grain from 5 m length of two rows (g/7.5 m^2)
Straw yield	SYD	vegetative dry matter at maturity from 5 m length of 2 rows (g/7.5 m^2)
Biomass	BM	PYD + SYD (g/7.5 m^2)
Growth index	GI	[BM/(TFL + 10)]/7.5 (g m^{-2} d^{-1})
Harvest index	HI	100 * GYPS/BM (%)
Plant height	PH	cm from soil surface to top of primary panicle (average of 10 plants/plot)
Seed mass	TSM	mass of 1000 seeds (g)
Panicle length	PLN	mean length of ten primary panicles (cm)
Plant count/plot	PCP	number of plants from 5 m length of two rows (2-3 weeks after thinning)
Panicle (head) count/plot	HCP	number of panicles from two rows 5-m length (taken two weeks before harvesting)
Tiller number	TNO	HCP/PCP (# $plant^{-1}$)
Grain yield/day	GYPD	GYPS/(TFL + 25) (g/7.5 m^2/day)

PYD, GYPS, BM, SYD, and GYPD were converted to kg ha^{-1} by multiplying by a factor of 1.333

Results

RESULTS

Table 6 presents the combined analyses of variance according to model II of Gardner and Eberhart (1966) for nine characters measured over one to five environments. The analyses showed highly significant differences among entries for all traits studied. The entry x environment interactions were highly significant for all traits except growth index and biomass. Sources of variation among parental populations (V_i) were highly significant ($P<0.01$) for all traits. In all cases, the major source of variation among entries sums of squares were variety effects (V_i), which varied from 51% for growth index to 92% for time to flowering and plant height. Heterosis effects (h_{ij}) were significant for grain yield per season, time to flowering, panicle length, tiller number, and thousand seed mass. Average heterosis effects were nonsignificant for most characters while variety heterosis and/or specific heterosis effects were significant for time to flowering, plant height, panicle length, tiller number, and biomass. This showed that both variety heterosis and specific heterosis are more important than average heterosis effects, indicating that additive genetic effects are more important than dominance in controlling most of these traits. Analysis II of Gardner and Eberhart (1966) is related to Analysis III of Lonnquist and Gardner (1961) in such a way that general combining ability (GCA, g_i) = $\frac{1}{2}V_i + h_i$ and specific heterosis (s_{ij}) = specific combining ability (SCA) (Eberhart and Gardner, 1966; Hallauer and Miranda, 1988). The predominance of GCA and the significant variety effects (V_i) suggest that the variation among crosses was due mainly to additive rather than nonadditive gene effects, which means that these traits can be improved by

recurrent selection and that hybrid cultivars based on these populations would not have clear performance advantages over open-pollinated cultivars.

The coefficient of variability for most of the characters studied were <13% for individual environments. Tiller number and panicle length showed the highest coefficients of variation, >18% for most environments (data not shown).

Grain yield per season

The combined analysis of variance for grain yield per season (kg ha^{-1}) showed that 75% of the sum of squares among entries was attributed to variety effects (V_i) and 25% could be explained by heterosis effects (h_{ij}) (Table 6). Average heterosis was significant ($P<0.05$) for grain yield per season, but specific heterosis (s_{ij}) was the most important component of total heterosis (h_{ij}). This result suggest that both additive and nonadditive effects are involved in the expression of grain yield per season. Similar results were found by Miranda and Vencovsky (1984) and Crossa *et al.* (1990) in maize.

The population means across five environments ranged from 1750 kg ha^{-1} for LHGP to 3160 kg ha^{-1} for ICMV 91059 (Table 7). ICMV 155, ICMP 87307, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059 had above-average yields. The parental populations having significantly positive variety effects and positive GCA effects were ICMV 155, ICMP 91751, ICMP 92591, and ICMV 91059. Both ICMP 87307 and SenPop had positive, but nonsignificant, variety and GCA effects. Lower yielding populations were LHGP, ICMP 87200, AfPop 90, NWC C2, and AfPop 88. These also had negative variety effects and negative GCA effects except ICMP 87200 which had nonsignificant positive

GCA effects. LHGP had significantly negative variety and GCA effects and ICMP 87200 had significant negative variety effects. SenPop had the largest positive GCA effects (167 kg ha^{-1}) and the second largest were those of ICMV 91059 (137 kg ha^{-1}). Differences in GCA effects indicate SenPop had a significantly higher frequency of favorable alleles for grain yield per season than LHGP.

The mean grain yield per season for crosses (Table 7) ranged from 1970 kg ha^{-1} for the cross AfPop 88 x LHGP to 3220 kg ha^{-1} for the cross ICMP 87200 x ICMV 91059. There were no significant differences between the four top-yielding crosses. Six of the crosses numerically outyielded the highest yielding controls (ICMP 93308 (IVC C8), ICMP 93752 (SRC II C2), and ICMP 91507 (NELC C7), with yields of 3160, 3140, and 3050 kg ha^{-1}, respectively). These six crosses were ICMP 87200 x ICMV 91059, ICMP 92591 x SenPop, AfPop 90 x ICMV 91059, ICMP 87307 x ICMP 87200, ICMP 91751 x ICMP 92591, and SenPop x ICMV 91059. This result is in line with the previous findings that the best combinations come from relatively distantly related populations. Synthetic variety ICMV 91059, an elite material only distantly related to the other parents in this study, was the parent in three of the above mentioned crosses. ICMP 87200, ICMP 92591 (Lubasi) and SenPop were each parents of two of these six top crosses and in each case were only distantly related to the other parent involved in the cross. Further, each of these top six crosses, with the possible exception of ICMP 92591 x SenPop, had one agronomically elite parent. This, in part, explains the superiority of these crosses. Crosses ICMV 155 x LHGP and ICMP 87307 x ICMP 87200 both had highly significant positive SCA effects, but only in the latter case did this result in cross performance better

than the better parent. AfPop 88 x LHGP had highly significant negative SCA effects, performing even more poorly than the expected--a clear example of negative heterosis. Other crosses having positive significant SCA effects were ICMV 155 x AfPop 90, ICMP 87200 x ICMV 91059, AfPop 90 x LHGP, AfPop 90 x ICMV 91059, and LHGP x SenPop. Despite the relatively low mean grain yield of ICMP 87200 per se, it had significant positive specific combining ability with ICMV 91059 and ICMP 87307 that in both cases resulted in high-yielding crosses (included among the top six mentioned above) performing better than their best parent. AfPop 90 was another parent with poor performance per se for grain yield per season with significant positive SCA contributing to superior cross performance. These two non-elite parents appear to carry genes that can combine well with those in the elite populations in hybrid combinations, but that might not be so useful in a breeding program targeting development of only open-pollinated cultivars. Crosses that showed significant negative SCA effects were ICMV 155 x ICMP 92591, ICMP 87307 x ICMV 91059, and ICMP 87200 x AfPop 90, and in each case this might indicate some closer than average degree of relationship of the parents. These significant SCA effects indicated that these crosses had grain yield different from that indicated by GCA effects of their parents. A breeding program targeting development of hybrid cultivars could more effectively exploit the significant positive SCA effects detected here than could a program targeting development of open-pollinated varieties.

The experiment was conducted over five environments to estimate entry x environment interactions and to obtain estimates of genetic parameters unbiased by

interactions with a specific environment. As indicated in Table 6, entry x environment interactions were found to be significant for most traits, but had greater importance for grain yield per season. The entry x environment interaction sums of squares were equally important to those of entries for grain yield per season, limiting the utility of these across-environment results for selecting high yielding populations for specific environments. This was clear from the results of the individual environments (Appendices 1-5), which showed great variability in performance of parents and their crosses. The mean grain yield per season for the three rainy seasons (1993-1995) at Patancheru were comparable and higher than those under irrigated conditions at Bhavanisagar (1993) and Patancheru (1994 dry season). The overall mean for grain yield per season under Patancheru rainy season conditions were 3370, 3230, and 2950 kg ha^{-1} for 1993, 1994, and 1995, respectively (Appendices 2,4 and 5). The overall mean for grain yield per season for Bhavanisagar and the Patancheru 1994 dry season were 2120 and 2430 kg ha^{-1}, respectively (Appendices 1 and 3).

The parental population mean grain yield per season at Patancheru in the 1993 rainy season ranged from 2090 kg ha^{-1} for LHGP to 4010 kg ha^{-1} for ICMV 91059 (Appendix 2). The latter had the best performance of any entry for this trait under 1993 Patancheru conditions. Among the parents in this environment, only LHGP and NWC C2 had mean grain yield per season lower than 3000 kg ha^{-1}, and both had significant negative variety effects and negative GCA effects.

The mean grain yield per season for the parental populations in the Patancheru 1994 rainy season ranged from 1940 kg ha^{-1} for LHGP to 3720 kg ha^{-1} for ICMV 91059

(Appendix 4), whereas for the Patancheru 1995 rainy season it ranged from 1580 kg ha^{-1} for LHGP to 3340 kg ha^{-1} for ICMP 87200 (Appendix 5). The latter parent had good performance per se for grain yield per season only at Patancheru in the 1994 and 1995 rainy seasons. The mean grain yield per season for the parental populations ranged from 1100 kg ha^{-1} for ICMP 87200 to 2860 kg ha^{-1} for SenPop (Appendix 1) under 1993 Bhavanisagar conditions while in the Patancheru 1994 dry season parental means varied from 1940 kg ha^{-1} for ICMP 87200 to 2740 kg ha^{-1} for ICMV 91059 (Appendix 2). This clearly indicates that these populations behaved differently in these different environments. The same holds true for performance of the crosses. These variations in grain yield performance under different environmental conditions were attributed to variation in time to flowering under these environments, in part due to differences in photoperiod response, day length differences between the Patancheru rainy seasons and the other two environments (Bhavanisagar and Patancheru dry season). The time to flowering and plant height under longer day length Patancheru rainy season conditions were greater than those in the shorter day length Bhavanisagar and Patancheru dry season conditions (data not shown).

Grain yield per day

A useful way to evaluate the possibility of combining good yield performance with earliness is by calculating grain yield on a per day basis. This measurement is actually a way of accounting for yield differences due to maturity differences. Early varieties

having high yield per day are potentially capable of producing a high yield in shorter time and can escape terminal drought stress to give good yield even under moisture stress conditions. The analysis of variance (Table 6) revealed that there were highly significant differences among entries and highly significant entry x environment interactions for grain yield per day. The sums of squares for entries were approximately twice as large as these for the entry x environment interaction, indicating that much more can be gained by analyzing the across-locations results for this trait than in case of grain yield per season from these same trials. The variety effects (V_i) were highly significant and accounted for 86% of the variation of the entry sums of squares. The total heterosis (h_{ij}) and all its components were nonsignificant.

The parental population means across five environments for grain yield per day ranged from 20 kg ha^{-1} d^{-1} for LHGP to 43 kg ha^{-1} d^{-1} for the reselected synthetic variety ICMV 91059 (Table 8). ICMV 155 and ICMP 91751 were the second (42 kg ha^{-1} d^{-1}) and the third (40 kg ha^{-1} d^{-1}) highest yielding populations, respectively. The populations having significant positive variety effects and positive GCA were ICMV 155, ICMP 91751, ICMP 92591, and ICMV 91059, whereas SenPop and ICMP 87307 had positive variety and GCA effects. LHGP had highly significant negative variety and GCA effects indicating its poor potential for grain yield per day and poor combining ability. This was attributed to lower mean grain yield per season and very late maturity of this parent, both of which were reflected in its crosses.

The mean grain yield per day for crosses (Table 8) ranged from 23 kg ha^{-1} d^{-1} for AfPop 88 x LHGP to 43 kg ha^{-1} d^{-1} for ICMP 91751 x ICMP 92591. The crosses showing

significant positive specific combining ability (specific heterosis) are ICMV 155 x LHGP, AfPop 90 x LHGP, LHGP x SenPop, ICMP 87307 x ICMP 87200, ICMP 87200 x ICMV 91059, and AfPop 90 x ICMV 91059. However, only in case of ICMP 87307 x ICMP 87200, did this positive SCA contribute to cross performance superior to that of the better parent. LHGP, which had significantly negative variety and GCA effects, was involved in three of the six crosses having significant positive SCA but none of these crosses was in fact very good for this trait. ICMV 91059, which had significant positive variety effects and positive GCA effects, was involved in two crosses with high SCA. In this case the crosses were both good, but neither gave a performance superior to ICMV 91059 itself. AfPop 90 and ICMP 87200 were also involved in 2 crosses with high SCA, but had significant negative varietal effects. Crosses showing significant negative SCA are ICMV 155 x ICMP 92591 and ICMP 87307 x ICMV 91059. The cross AfPop 88 x LHGP showed a high significant negative SCA effects. This was perhaps due to the lateness of both parental populations. These results revealed that the two feeder populations based on African breeding materials (AfPop 88 and AfPop 90) together with LHGP have lower grain yield per day per se and lower potential in crosses. If these results are upheld when the selfed crosses are analyzed in future, it would not be recommended to include these parents as components of medium-late populations for recurrent selection programs having short to medium time horizons.

The mean performance per se of the populations and their performance in crosses indicated that ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059 are the better general combiners with high genetic potential for both grain yield per season and

grain yield per day, and hence are the most suitable parents for making new composite populations with high agronomic potential.

Total biomass

The combined analysis of variance across two environments showed that for total biomass 54% of the sum of squares among entries was attributed to variety effects (V_i) (Table 6). The variety effects were highly significant. The total heterosis (h_{ij}) and average heterosis ($\bar{h}$) were nonsignificant, whereas variety heterosis (h_i) and specific heterosis (s_{ij}) were significant at $P<0.01$ and $P<0.05$, respectively. The entry x environment interaction was nonsignificant, and this showed that biomass was less affected by environmental variation than grain yield per season and grain yield per day, but this is perhaps because it was only evaluated under two relatively similar seasons. Specific heterosis accounted for 62% of the variation of the heterosis sums of squares and 35% was attributed to variety heterosis. Average heterosis was negligible. The significant high variety effects and the relatively high variety heterosis effects indicated that additive genetic effects were more important than nonadditive genetic effects in the inheritance of biomass.

The mean total biomass production for parent populations varied from 9010 kg ha^{-1} for ICMP 91751 to 13450 kg ha^{-1} for LHGP (Table 9). LHGP and AfPop 90 had high positive variety and GCA effects for this character while all other populations except AfPop 88 had negative variety effects. Except for ICMP 91751, these negative variety effects were not significantly different from zero, although in all cases they were

significantly less than the variety effects of AfPop 90 and LHGP. The populations having positive GCA effects were ICMP 87200, AfPop 88, AfPop 90, LHGP, and SenPop. Of these, only SenPop has some degree of agronomic eliteness for Indian conditions. All the other populations had nonsignificant negative GCA effects for this character.

The mean biomass production for the crosses varied from 8530 kg ha^{-1} for ICMV 155 x ICMV 91059 to 11010 kg ha^{-1} for AfPop 90 x LHGP. Among the 55 crosses only two crosses had significant positive SCA effects and these were AfPop 88 x SenPop and ICMV 155 x ICMP 87307. In the former case, the hybrid had the second highest biomass among crosses, so it may be worthwhile to exploit SCA for biomass in hybrids. The cross LHGP x SenPop had highly significant negative SCA effects. NWC C2 x AfPop 90 also had significant negative SCA effects. The high biomass production in crosses involving LHGP, AfPop 90, AfPop 88, SenPop, and ICMP 87200 indicated that these populations contain favorable alleles for this character that might be of use in breeding single-cut forage cultivars.

Growth index

The analysis of variance across two environments (Table 6) revealed highly significant differences among entries, and nonsignificant entry x environment interactions for growth index. The latter was perhaps due to this trait having only been evaluated in two similar Patancheru rainy season environments. Among the sources of variation among entries, only variety effects (V_i) were highly significant. The variety sum of squares accounted for 51% of the variations among the entries sums of squares. This indicated variety and

heterosis effects were equally important for this trait, which in turn suggested that both additive and nonadditive genetic effects were involved in the inheritance of this trait. The mean growth index for parental populations varied from 8.0 g m^{-2} d^{-1} for ICMV 155 and ICMP 91751 to 12.4 g m^{-2} d^{-1} for LHGP (Table 10 and Appendix 6). AfPop 90 and LHGP had highly significant positive variety effects for growth index, but they had nonsignificant positive GCA effects. AfPop 88, AfPop 90, LHGP and SenPop had above average mean growth indices and all had positive GCA effects except AfPop 88. Therefore, these populations are good general combiners for this character. One unexpected result was that ICMP 87200 had both poor mean growth index per se and negative variety effects but had positive GCA effects reflecting its positive heterotic performance in crosses. This parent apparently has some nonadditive genes for this trait that could be exploited in hybrids. Only ICMP 91751 had significantly negative variety effects for growth index. On the other hand, all other parental populations had below average mean growth indices. Correlation analysis (Table 11) of parental variety effects (V_i) GCA effects (g_i) showed a significant association ($r = 0.92$) for growth index, which suggests the predominant role of additive genetic effects in controlling this trait. This result seems to conflict with that of Lynch *et al.* (1995) who reported additive x additive epistatic effects to be of greatest importance in the inheritance of growth index measured at maturity (GI2 in their study) in pearl millet. Future analysis of the data from selfed parents and crosses for this trait may resolve this apparent conflict.

The mean growth indices for the crosses varied from 7.8 g m^{-2} d^{-1} for ICMP 87307 x ICMP 92591 and LHGP x SenPop to 10.7 g m^{-2} d^{-1} for ICMP 87200 x LHGP. Twenty-six

of the 55 crosses had mean growth indices above average. LHGP was involved as parent in eight, ICMP 87200 in seven, and AfPop 90 and SenPop were each involved in six of the above mentioned crosses. These four parents are suggested to be suitable for developing populations having high mean growth indices. ICMP 87200 had a negative variety effects (V_i) and poor performance per se, but it performs very well in crosses, and this might be due to complex nonallelic interactions and some degree of dominance at one or more loci. Therefore, this parent might be used for production of forage hybrid cultivars if they are needed by the breeding programs in the future. The crosses having significantly positive specific heterosis (SCA, s_{ij}) were AfPop 88 x SenPop, ICMP 92591 x SenPop, and LHGP x ICMV 91059, whereas, ICMP 87200 x ICMP 92591, NWC C2 x LHGP, and LHGP X SenPop had significantly negative SCA effects for growth index. The parents in each of the former three crosses were more genetic divergent which was reflected in high heterotic effects for this trait in their hybrids. The three latter crosses showed negative SCA because parents in each were less divergent and may have some closer degree of relationship which was reflected in their poor hybrid performance. These results agree with Moll *et al.* (1962), Moll *et al.* (1965), who reported heterosis in maize to increase with increased genetic divergence of the parent populations over a rather wide range of diversity.

Time to flowering

The analysis of variance for time to 75% flowering (Table 6) revealed highly significant differences among entries and among entry x environment interactions. The proportion

of variation due to entry x environment interaction was small (the interaction sums of squares was approximately 10% of the entries sums of squares), so it is justifiable to focus attention here only on across-environment means. The variety effects and the total heterosis effects were also highly significant. This analysis showed that 92% of the sums of squares among entries was attributable to variety effects (V_i). Specific heterosis (s_{ij}) was the most important component of the total heterosis (h_{ij}), accounting for 50% of this. Average heterosis ($\bar{h}$), variety heterosis (h_i), and specific heterosis (s_{ij}) were also highly significant. The mean difference in time to flowering between the earliest and the latest flowering parents was 24 days (Table 10 and Appendix 7). The varieties having significant desirable negative GCA and variety effects (earliness) were ICMV 155, ICMP 91751, ICMP 92591, SenPop and ICMV 91059, indicating their potential for breeding earlier maturing composite populations (in the range of maturities included in this study). LHGP, together with the two feeder populations AfPop 88 and AfPop 90, had significantly high positive GCA and variety effects, indicating that these populations contain genes for lateness that are undesirable in grain or dual-purpose materials for Indian conditions. These results suggest that these three populations are unsuitable materials from which to form improved composite populations with full-season maturity for Indian conditions (comparable to ICMV 155), and should be crossed with earlier materials if they are to be used in expanding the genetic base of elite composites for southern Asia. For crosses, the difference between the earliest and latest cross was less by 7 days than that of the parents, suggesting some degree of dominance for earliness. There was a high correlation between parental varietal (V_i) and GCA (g_i) effects (Table 11), which

suggests predominance of additive genetic effects for the inheritance of time to flowering. Similar results were obtained by Navale *et al.* (1991), Ouendeba *et al.* (1993), and Lynch *et al.* (1995) in pearl millet populations.

Plant height

As shown in Table 6, entry x environment interactions were highly significant for plant height, but their sums of squares totalled only 30% those for entries. Therefore the analysis of genetic effects was again confined to across-environment means. The combined analysis of variance for plant height indicated that V_i and h_{ij} effects accounted for 92% and 8% of the variability among entries, respectively. Variety effects were highly significant whereas heterosis effects were nonsignificant. Among the components of heterosis only variety heterosis (h_i) effects were highly significant. Plant height for parental populations varied from 210 cm for ICMV 155 to 270 cm for LHGP (Table 10 and Appendix 8). Populations having significantly negative GCA and variety effects were ICMV 155, ICMP 91751, and ICMV 91059, which indicated that these are excellent combiners for the relatively shorter plant height required under Indian conditions. LHGP and the two feeder populations AfPop 88 and AfPop 90 were the tallest among all parental populations and they had significant positive variety and GCA effects. The high correlation (r = 0.95) between the parental varietal effects and GCA effects (Table 11) suggests the predominance of additive genetic effects for this character. Medium plant height and strong stalks are useful in regions characterized by strong winds that can cause heavy production losses due to lodging. ICMV 155, ICMP 91751, and ICMV 91059

had significant negative variety and GCA effects for plant height, suggesting that they could be used as parents to breed for medium plant height to reduce lodging losses.

Mean plant heights for crosses varied from 210 cm for ICMV 155 x ICMV 91059 and ICMP 91751 x ICMV 91059 to 270 cm for AfPop 88 x LHGP. Twenty-six of the 55 crosses showed significant negative specific combining ability (s_{ij}) (Appendix 8). Six crosses had mean plant heights <220 cm. ICMV 155 was involved in four of them and ICMV 91059 involved in three. Six taller crosses had mean plant heights >250 cm. LHGP was the parent of four of these, AfPop 88 of three and AfPop 90 of two of these taller crosses.

Panicle length

The analysis of variance for panicle length (Table 6) revealed highly significant differences for both entries and entry x environment interactions, but the entry x environment sums of squares accounted for only 12% of the total for entries and interactions. This indicates the across-environment analysis should give reliable estimates of genetic effects. Among entries, both variety and heterosis effects were highly significant. The mean panicle length for parental populations varied from 25 cm for ICMV 155 and ICMV 91059 to 45 cm for LHGP (Table 10 and Appendix 9). LHGP and the two feeder populations had significant positive variety (V_i) and GCA (g_i) effects, indicating their good combining ability for this trait. Populations having significant negative GCA and variety effects for panicle length were ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059.

Panicle length means for crosses varied from 25 cm for ICMP 92591 x ICMV 91059 to 42 cm for AfPop 90 x LHGP (Appendix 9). The Long Headed Gene Pool (LHGP) from the Genetic Resources Division at ICRISAT Asia Center was involved in the four crosses having longer panicles, but the grain yield of these crosses were below average. This indicates there was little contribution of this increased panicle length to grain yield, perhaps due to poor seed set on longer panicles due to their delayed flowering. Specific heterosis values were highly significant whereas variety heterosis (h_i) and average heterosis ($\bar{h}$) were nonsignificant. The parental varietal (V_i) and GCA (g_i) effects for panicle length were highly correlated (r = 0.98) (Table 11) indicating the predominant role of additive genetic effects in controlling this trait.

Tiller number

The analysis of variance over four environments (Table 6) revealed highly significant entries effects and entry x environment interaction effects. The entries sums of squares were more than twice that of those for entry x environment interactions for this trait. This indicates that variation due to environment interactions were less important compared to variation among entries. Among entries, across environments, the variety (V_i) and heterosis (h_{ij}) effects were highly significant, and accounted for 59 and 41% of the variation among entries sum of squares, respectively. Variety heterosis (h_i) and specific heterosis (s_{ij}) were significant whereas average heterosis ($\bar{h}$) was not significant.

The correlation analysis (Table 11) for tiller number showed that the parental varietal effects (V_i) and GCA effects (g_i) were low to moderately correlated (r = 0.41) suggesting

both additive and nonadditive gene effects to be important for the inheritance of this trait. The mean tiller number for the parental populations varied from 1.1 for AfPop 88, AfPop 90, and LHGP to 2.5 for ICMP 87200 (Table 10 and Appendix 10). Although ICMV 155, ICMP 87307, ICMP 91751, NWC C2, and ICMV 91059 had positive GCA effects for this trait, only those of ICMV 155 and NWC C2 were statistically significant. However, all five of these parental populations had GCA effects for tiller number significantly greater than those of AfPop 88, AfPop 90 and LHGP.

Thousand seed mass

The analysis of variance (Table 6) for thousand seed mass in the Patancheru 1995 rainy season revealed highly significant differences for varieties and heterosis effects. All components of heterosis ($\bar{h}$, h_i, and s_{ij}) were nonsignificant. The mean thousand seed mass for parental populations varied from 7.7 g for AfPop 90 to 11.6 g for ICMV 155 (Table 10 and Appendix 11). Parental populations having significantly positive variety effects were ICMV 155, ICMP 91751, and ICMP 92591. Populations with significantly negative variety effects were ICMP 87200, AfPop 90, and LHGP. The GCA effects for parental populations were not significantly different from zero except in case of LHGP, which had significantly negative GCA effects.

The mean thousand seed mass for crosses ranged from 8 g for AfPop 90 x LHGP to 12 g for five different crosses. ICMV 155 and SenPop were each parents of three of the five crosses having 12 g mean thousand seed mass (Appendix 11). High correlation (r

= 0.82) between parental varietal and GCA effects (Table 11), indicated that additive genetic effects were more important than nonadditive effects in the inheritance of this trait. Balzor Singh and Govila (1989) showed that the highest grain yield was produced by hybrids involving lines with bold grains, and also observed a high correlation between 1000-seed mass and yield (r = 0.79). Results on thousand seed mass from eleven pearl millet populations and their F_1 hybrids in the present study indicated that varieties ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059 are suitable parents for improving grain size.

Relationships between traits

Correlations (Table 12) of parental variety effects (V_i) for the nine traits in this study, revealed that grain yield per season and grain yield per day were significantly positively correlated, as expected, and both of them were positively correlated with thousand seed mass. Varietal effects for tiller number were significantly positively correlated with those for grain yield per day, but uncorrelated with those for grain yield per season. Varietal effects for time to flowering, plant height, panicle length, biomass, and growth index were negatively correlated with those for grain yield (both per season and per day). This indicates that in this set of materials, lateness is strongly associated with high biomass production, high vegetative growth rate (growth index), tall plant height, longer panicles, relatively fewer tillers, and low grain yield.

The patterns of correlations for parental GCA values were generally similar to those of variety effects for most traits, although in most cases the correlation coefficients were less than those for variety effects. GCA effects for tiller number had significant positive correlations with those for grain yield per season, grain yield per day, and thousand seed mass but significantly negatively correlated with those for other traits.

Table 6. Mean squares of some traits for eleven pearl millet populations and their 55 diallel crosses tested across one to five environments[1] in India.

Source	d.f.	Grain yield per season (kg ha^{-1})	Grain yield per day (kg ha^{-1})	Time to flowering (d)	Plant height (cm)	Panicle length (cm)	d.f.	Tiller number
Environments (E)	4						3	
Replication/E	10						8	
Entries	65	78 956**	22.55**	16.48**	229**	17.5**	65	0.061**
Varieties (V_i)	10	385 658**	125.62**	99.01**	1368**	103.6**	10	0.235**
Heterosis (h_{ij})	55	23 192*	3.81	1.48**	22	1.8**	55	0.030**
Average ($\bar{h}$)	1	83 616*	11.31	6.52**	12	0.9	1	0.003
Variety (h_i)	10	16 662	3.52	3.40**	33**	0.9	10	0.101**
Specific (s_{ij})	44	23 305	3.71	0.93**	20	2.1**	44	0.015*
Entries x E	259 (1)[§]	16 913**	3.30**	0.56**	20**	0.6**	194 (1)	0.010**
Pooled error	648 (2)	12 236	2.14	0.13	11	0.5	515 (5)	0.006

*, ** significant at $P<0.05$ and $P<0.01$, respectively.

[§] The values in parentheses indicate missing observations.

[1] Environments are Bhavanisagar 1993 rainy season; and Patancheru 1993 rainy season, 1994 dry season, 1994 rainy season, and 1995 rainy season, except for the trait tiller number, which was not evaluated at Bhavanisagar.

Table 6. (continued) Mean squares of nine traits from eleven pearl millet populations and their 55 diallel crosses tested across one to five environments in India.

Source	d.f.	Biomass (kg ha^{-1})	Growth index (g m^{-2} d^{-1})	d.f.	TSM (g)
Environments (E)	1				
Replication/E	4			2	
Entries	65	604 145**	67.7**	65	0.7**
Varieties (V_i)	10	2 109 850**	226.1**	10	3.5**
Heterosis (h_{ij})	55	330 362	38.9	55	0.3**
Average ($\bar{h}$)	1	661 504	11.3	1	0.1
Variety (h_i)	10	632 166**	46.9	10	0.3
Specific (s_{ij})	44	254 247*	37.7	44	0.2
Entries x E	65	220 061	28.3		
Pooled error	260	182 833	30.3	130	0.2

*, ** significant at $P<0.05$ and $P<0.01$, respectively.

[1] Biomass and growth index measured at Patancheru 1993 and 1995 rainy seasons.

[2] TSM (thousand seed mass) in Patancheru 1995 rainy season only.

Table 7. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across five environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**3000**	2940	2890	2910	2710	2900	3060	2760	2700	2980	2900	**45**	**260**
2	2	**2900**	3030	3170	2710	2820	2810	3100	2560	2930	2840	**64**	**165**
3	-66	50	**2970**	2940	2960	2900	2890	3170	2310	2980	3000	**80**	**230**
4	9	259	12	**2430**	2800	2780	2630	2830	2240	2980	3220	**18**	**-308**
5	-123	-143	95	-3	**2660**	2820	2740	3040	2240	3020	2880	**-46**	**-84**
6	99	3	60	9	114	**2670**	2650	2820	1970	2980	3000	**-79**	**-70**
7	196	-79	-9	-214	-34	-97	**2650**	2830	2630	2830	3180	**-13**	**-84**
8	-200	125	169	-102	172	-21	-77	**3030**	2410	3200	2920	**81**	**293**
9	267	112	-157	-162	-99	-338	255	-51	**1940**	2780	2470	**-450**	**-989**
10	-66	-130	-101	-40	63	59	-158	117	224	**2900**	3170	**167**	**166**
11	-118	-198	-54	233	-42	111	218	-131	-50	32	**3160**	**137**	**420**

[1] 1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.

Mean = 2820, SE(mean) = ±14, SE(g_i) = ±116, SE(V_i) = ±105, SE(s_{ij}) = ±99.

Table 8. Mean grain yield per day (kg ha^{-1} d^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield per day (kg ha^{-1} d^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across five environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**42**	39	39	39	36	37	39	37	34	41	41	**1.8**	**7.0**
2	-0.1	**38**	41	41	35	36	35	41	31	38	37	**1.0**	**2.4**
3	-1.5	0.5	**40**	39	40	37	37	43	29	41	41	**2.5**	**5.0**
4	0.5	3.2	0.1	**30**	36	35	33	39	26	38	42	**0.1**	**-5.0**
5	-1.9	-1.9	1.3	-0.3	**34**	35	34	39	27	39	38	**-0.7**	**-1.4**
6	1.2	0.1	0.3	0.3	1.8	**33**	31	36	23	37	39	**-2.1**	**-2.7**
7	2.2	-0.8	0.1	-1.7	-0.4	-1.3	**32**	35	30	35	40	**-1.7**	**-3.8**
8	-2.9	2.2	2.5	-1.3	2.2	-0.1	-1.6	**39**	30	42	39	**1.6**	**3.9**
9	3.1	1.6	-1.8	-2.5	-0.7	-3.7	2.7	-0.4	**20**	34	30	**-7.8**	**-15.1**
10	-0.2	-2.0	-0.8	-1.2	0.6	0.0	-1.9	1.4	3.0	**38**	42	**2.5**	**2.4**
11	-0.4	-3.0	-0.6	2.9	-0.7	1.4	2.8	-1.9	-1.4	1.0	**43**	**2.8**	**7.6**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 36, SE(mean) = $\pm$0.2, SE(g_i) = $\pm$1.5, SE(V_i) = $\pm$1.4, SE(s_{ij}) = $\pm$1.3.

Table 9. Mean biomass (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean biomass (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across two environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**9060**	9720	8550	9780	8890	8860	9820	8810	10150	9020	8530	**-419**	**-795**
2	790	**9250**	9170	10020	8980	8990	8990	8800	9720	9670	8820	**-234**	**-607**
3	-390	50	**9010**	9100	9850	9530	10270	9190	9500	9160	9450	**-238**	**-845**
4	380	430	-490	**9540**	9840	9690	9810	8770	10780	10280	9930	**235**	**-323**
5	-110	-200	670	190	**9180**	10250	8940	9510	9320	9710	9070	**-171**	**-675**
6	-460	-510	20	-280	680	**9880**	10140	9010	10480	10890	9410	**149**	**24**
7	140	20	410	-530	-990	-110	**11280**	9780	11010	10320	10540	**514**	**1417**
8	-60	-250	140	-740	400	-420	-10	**9230**	9860	10160	9230	**-308**	**-629**
9	520	-90	-310	500	-560	280	450	120	**13450**	8940	10270	**459**	**3595**
10	-320	150	-360	290	120	980	40	710	-1280	**9340**	9260	**167**	**-520**
11	-490	-380	260	260	-200	-180	590	100	380	-340	**9220**	**-154**	**-640**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 9640, SE(mean) = ±53, SE(g_i) = ±449, SE(V_i) = ±408, SE(s_{ij}) = ±382.

Table 10. Mean, GCA (g_i), and variety (V_i) effects of six traits from eleven pearl millet parental populations across five environments[1].

	Time to flowering (days)			Plant height (cm)			Panicle length (cm)		
Parents	**Mean**	**g_i**	**V_i**	**Mean**	**g_i**	**V_i**	**Mean**	**g_i**	**V_i**
ICMV 155	46	-2.9**	-8.1**	210	-12**	-24**	25	-2.9**	-5.1**
ICMP 87307	52	-0.6	-2.1**	225	-3	-9**	27	-1.1	-3.8**
ICMP 91751	50	-3.1**	-4.9**	215	-12**	-22**	28	-1.5*	-2.8**
ICMP 87200	56	0.5	1.2**	235	5	0	31	0.3	0.5
NWC C2	54	0.1	-0.5	230	-2	-6	28	-0.3	-2.4**
AfPop 88	57	2.5**	3.0**	260	11**	25**	35	2.0**	4.6**
AfPop 90	59	3.1**	5.0**	250	12**	18**	36	3.0**	5.1**
ICMP 92591	52	-1.3*	-2.0**	240	-5	6	28	-1.5*	-2.2**
LHGP	70	5.0**	15.8**	270	19**	36**	45	6.3**	14.4**
SenPop	52	-1.0*	-2.0**	230	-1	-5	27	-1.4*	-3.4**
ICMV 91059	49	-2.2**	-5.7**	215	-11**	-18**	25	-2.9**	-5.3**
SE (+/-)	0.05	0.38	0.35	0.4	3.4	3.1	0.1	0.71	0.65
General mean	54			236			30		

[1] Environments are Bhavanisagar 1993 rainy season; and Patancheru 1993 rainy season, 1994 dry season, 1994 rainy season, and 1995 rainy seasons.

*, ** indicate significantly different from zero at $P<0.05$ and $P<0.01$, respectively.

Table 10 (continued). Mean, GCA (g_i), and variety (V_i) effects of some traits from eleven pearl millet parental populations across five environments.

Parents	Tiller number[1]			Growth index[2] (g m^{-2} d^{-1})			Thousand seed mass[3] (g)		
	Mean	g_i	V_i	Mean	g_i	V_i	Mean	g_i	V_i
ICMV 155	1.7	0.18*	0.25**	8.0	-0.32	-0.94	11.6	0.68	1.45**
ICMP 87307	1.3	0.08	-0.20*	8.5	-0.25	-0.55	10.4	0.07	0.31
ICMP 91751	1.6	0.06	0.12	8.0	-0.20	-1.04*	11.4	0.57	1.28**
ICMP 87200	2.5	-0.01	1.03**	8.6	0.30	-0.47	8.9	-0.10	-1.22**
NWC C2	1.4	0.18*	-0.09	8.8	-0.18	-0.27	9.6	-0.34	-0.49
AfPop 88	1.1	-0.17*	-0.41**	9.1	-0.04	0.03	10.0	-0.28	-0.12
AfPop 90	1.1	-0.19**	-0.35**	10.5	0.26	1.45**	7.7	-0.68	-2.46**
ICMP 92591	1.4	-0.02	-0.04	8.3	-0.30	-0.75	11.1	0.37	0.98*
LHGP	1.1	-0.22**	-0.35**	12.4	0.70	3.41**	9.5	-0.95*	-0.59
SenPop	1.5	0.05	0.00	9.0	0.18	-0.04	10.4	0.33	0.31
ICMV 91059	1.5	0.06	0.06	8.2	-0.16	-0.84	10.7	0.32	0.55
SE (+/-)	0.01	0.08	0.09	0.07	0.58	0.52	0.05	0.42	0.39
General mean	1.5			8.9			10.2		

[1] Tiller number plant^{-1} determined at Patancheru only (1993 rainy season, 1994 dry season, 1994 rainy season, and 1995 rainy season).

[2] Growth index in Patancheru 1993 and 1995 rainy seasons.

[3] Thousand seed mass in Patancheru 1995 rainy season only.

Table 11. Correlations of estimates of parental varietal effects (V_i) with parental GCA effects (g_i).

Trait	V_i vs g_i
Grain yield per season	0.92**
Grain yield per day	0.94**
Biomass	0.77**
Plant height	0.95**
Panicle length	0.98**
Tiller number	0.41
Time to flowering	0.95**
Growth index	0.92**
Thousand seed mass	0.82**

Table 12. Correlation coefficients among nine traits for parental variety (V_i) and parental GCA (g_i) values of eleven parental populations.

	Trait								
Trait	**GYPS**	**GYPD**	**BM**	**TFL**	**PH**	**PLN**	**TNO**	**GI**	**TSM**
GYPD	0.98**† 0.97**‡								
BM	-0.86** -0.53	-0.87** -0.68*							
TFL	-0.93** -0.81**	-0.97** -0.92**	0.93** 0.85**						
PH	-0.76** -0.58	-0.85** -0.74**	0.81** 0.87**	0.92** 0.93**					
PLN	-0.90** -0.88**	-0.93** -0.96**	0.94** 0.83**	0.97** 0.96**	0.91** 0.85**				
TNO	0.11 0.60*	0.19 0.71*	-0.41 -0.81**	-0.37 -0.83**	-0.47 -0.82**	-0.38 -0.84**			
GI	-0.86** -0.84**	-0.89** -0.85**	0.98** 0.76**	0.94** 0.78**	0.82** 0.60*	0.92** 0.86**	-0.46 -0.66**		
TSM	0.56 0.79**	0.66* 0.89**	-0.54 -0.81**	-0.63* -0.96**	-0.60* -0.86**	-0.57 -0.92**	0.06 0.71*	-0.58 -0.74**	

† Variety effects (V_i) ‡ GCA effects (g_i)

GYPS = grain yield per season, GYPD = grain yield per day, BM = biomass, TFL = time to flower, PH = plant height, PLN = panicle length, TNO = tiller number, GI = growth index, TSM = thousand seed mass.

DISCUSSION AND CONCLUSIONS

DISCUSSION AND CONCLUSIONS

The results obtained from this study seem to be reasonably consistent with other data on pearl millet yields that have been analyzed and examined by the method suggested by Gardner and Eberhart (1966). Forming base populations by compositing varieties that exhibit high grain yield and considerable heterosis in crosses is certain to result in excellent base populations with substantial genetic variation. Subsequent progress from any selection scheme based on additive gene effects might well be expected to be good. Crosses among pearl millet populations in this study were characterized by low heterosis in most crosses for most characters. This indicates limited potential for hybrid cultivars based on crosses among the parental populations used here. The significant variety effects for all traits and nonsignificant heterosis effects for most traits suggests the predominant role of additive gene effects in these materials. These results agree with the findings of Singh *et al.* (1982) and Ouendeba *et al.* (1993). However, the nonsignificant average heterosis shown by most traits in this study is a good evidence for the predominant role of additive genetic effects but does not necessarily indicate lack of dominance. The large heterosis in certain crosses indicates that their parental populations are genetically more diverse than those of crosses that manifest little or no heterosis (Mungoma and Pollak, 1988). Crosses ICMP 87200 x ICMV 91059 and ICMP 92591 x SenPop had the highest grain yield and selection within such population crosses would ensure rapid progress in the development of high-yielding full-season open-pollinated varieties for peninsular India.

Zaveri (1982) indicated that additive genetic variance was the most important component of genetic variation in the diallel variety cross of pearl millet populations. Phul *et al.* (1978) and Rao (1979) working on the PSB-3 population (a population generated by intermating 10 inbred lines in a diallel fashion) reported equal importance of additive and dominance components for grain yield, panicle length, days to flowering, and plant height with degrees of dominance in the range of complete to over dominance. Sharma (1978) also reported greater role of additive gene effects for days to flowering, plant height, and panicle length in composite populations of pearl millet.

Most previous genetic studies on pearl millet that support the predominance of additive genetic effects for various traits were conducted on inbred populations, with respect to days to flowering: Girgla (1975); Srinivasan *et al.* (1978); Govil *et al.* (1978); Singh *et al.* (1990), plant height: Gupta (1978); Sharma (1978); Ouendeba *et al.* (1993); Lynch *et al.* (1995), tiller number: Girgla (1975); Govil *et al.* (1978); Mehndiratta (1980); Sharma *et al.* (1987b), panicle length: Jain *et al.* (1961); Gupta and Singh (1971); Girgila (1975); Gupta (1978); Sharma (1978); Singh *et al.* (1978); Ouendeba *et al.* (1993), grain yield: Jindla (1981); Singh *et al.* (1982); Navale *et al.* (1991); Ouendeba *et al.* (1993), and found to be nonadditive by Girgila (1975); Govil *et al.* (1978); Mehndiratta (1980), and found to be additive and nonadditive by Ahluwalia *et al.* (1962); Mukherji *et al.* (1980, 1981); Tyagi *et al.* (1982); Kapoor *et al.* (1982), thousand seed mass: Phul and Gill (1970); Srinivasan *et al.* (1978); Jindla (1981).

Dhillon *et al.* (1977) showed from evaluation of lines from the world germplasm collection that seed size was the most important yield component. This trait, as well as

tiller number per plant, should be considered when selecting high yielding cultivars (Ouendeba *et al.*, 1993). Based on their mean performance per se and performance in crosses for thousand seed mass ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059 are the best parents included in this study. Their positive GCA effects and their high mean performance in crosses suggest that these would be suitable parents for a breeding program aimed at breeding open-pollinated cultivars with large seed size. However, other germplasm, breeding populations, and released cultivars with even larger seed size are available (e.g., Witcombe *et al.*, 1995).

Relevance to applied population improvement

The effectiveness of a population improvement program depends largely on the presence of additive genetic variance. Recurrent selection of superior individuals or families and their recombination to form an improved population should increase the frequency of favorable alleles and increase the chance of extracting new superior genetic combinations for use as cultivars or in hybrids. For efficient interpopulation improvement, the selection of cross mean(s) should be at the highest level possible accompanied by maximum additive genetic variation with each population (Lonnquist and Gardner, 1961; Sprague and Eberhart, 1977; Gardner, 1978). In the present study, a large amount of variability was observed for most of the traits suggesting there is scope for the efficient improvement of them in composite populations based on parents included here.

The information provided by this study is very useful to pearl millet breeding programs in Africa and India. The genetic constants estimated using the Gardner-Eberhart Analysis II provide indirect evidence on gene action as the dominance and additive genetic effects were determined jointly. The results revealed that genetic variability exists in the parental populations for a number of traits, and much of this variation was suggested to be additive in nature. This indicates that these populations are potentially suitable for recombination and developing elite composites having broad genetic base with high genetic variability for use in future recurrent selection programs. The populations having good performance per se and good performance in crosses for most traits were ICMV 155, ICMP 91751, ICMP 92591, SenPop, and ICMV 91059, which indicated that these populations possess good general combining ability for these traits. They should be exploited for developing one or more populations with improved agronomic performance. The feeder populations and the LHGP are the most poor combiners for most traits, but they were especially good combiners for panicle length and biomass production and growth index. They were generally very late, with few tillers, and had small grain size. For Indian conditions they may prove more suitable for use in fodder cultivars than in grain or dual-purpose (grain + straw) populations. The performance per se of ICMP 87200 and its GCA effects were generally poor, but its grain yield performance was excellent when crossed with ICMP 87307 and ICMV 91059. The latter cross gave the highest yield among all crosses across the five environments.

The results of this study confirmed significant positive correlations between variety effects for grain yield and thousand seed mass (Table 12), but found no correlation of

variety effects for grain yield with those for tiller number. However, significant positive correlations of grain yield with both tiller number and thousand seed mass were detected for GCA effects values. Variety effects for grain yield were significantly negative correlated with those for all other traits in this study. There are good indications that lateness is associated with tall plant height, long panicles, high biomass production, high vegetative growth rate, and reduced tillering in the parents included in this study.

Grain is the main purpose of pearl millet cultivation in Africa and Asia. However, the forage, or stover, remaining after grain harvest is an important secondary product in subsistence agriculture that is used for animal feed, fuel, or construction material (Andrews and Kumar, 1992). Thus vigorous, tall or semi-tall, relatively late varieties with a high biomass production are often preferred. LHGP and the feeder populations AfPop 88 and AfPop 90 appear suitable for such purposes in areas where their later maturity does not unduly increase the probability of terminal drought stress. However, they are not suitable for direct use in Indian conditions due to their late maturity.

Growth index (GI) is a measure of vegetative plant dry weight produced per unit of land area per day (grams per square meter per day). Selection for increased growth index (GI = kg ha^{-1} d^{-1}) was proposed by Takeda and Frey (1977) for increasing grain yield of cereals with short growth duration. In India, pearl millet is a short-duration cereal crop grown for grain and fodder, so its productivity may benefit from selection for increased GI. The growth index of pearl millet is quantitatively inherited (Bramel-Cox *et al.*, 1986; Rattunde *et al.*, 1989). Lynch *et al.* (1995) observed that additive x additive epistatic effects were of greatest importance for growth index measured at maturity, as

done in this study. However, the strong correlations between varietal and GCA effects (Table 11) of parents included here suggests that additive effects were predominant of this trait.

It is important for a breeder to know the relative magnitude of additive and dominance gene action to decide on the breeding methods and breeding strategy to use. However, selfed progenies from the variety crosses and the varieties themselves are needed to estimate additive and dominance effects separately from the population diallel and the complete Analysis I suggested by Gardner and Eberhart (1966) must be performed. Also, a mean square for deviations from the genetic model can then be used to test for epistasis and linkage effects. Data on selfed progenies of the parents and the hybrids are available from two environments (1994 and 1995 rainy seasons at Patancheru). Appropriate further analysis of these data should be undertaken to provide estimates of the above mentioned genetic parameters. Further, to get more precise information on the type of gene action and inbreeding depression, it is recommended that this trial be repeated in one more location for one or two seasons. The selected parental populations can be used in the national program of the Sudan as a source of genetic variability to improve local varieties for increasing productivity in future. This experiment can be repeated in the Sudan condition to see the performance of these materials in this new environment as compared to India.

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Appendices

APPENDICES

Appendix 1. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combing ability effects (s_{ij}, below diagonal) for their 55 crosses; Bhavanisagar, 1993 rainy season.

	Parental pearl millet populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**1970**	1730	2370	1790	2130	2490	2370	1650	1790	1960	2070	**-120**	**-1**
2	-473	**2310**	2420	2960	1890	1940	2080	2660	2420	2620	2300	**176**	**340**
3	348	98	**1930**	1940	2220	2060	2070	2420	1950	2290	1710	**3**	**-41**
4	-173	697	-149	**1100**	1900	2110	1730	2170	1660	2190	2470	**-57**	**-874**
5	196	-344	160	-101	**1630**	1970	2610	2880	820	1990	2240	**-86**	**-341**
6	556	-294	0	112	1	**2070**	2260	2440	1430	1990	1960	**-86**	**93**
7	228	-362	-195	-482	433	80	**1970**	2660	2160	2310	2280	**122**	**-1**
8	-590	126	60	-127	608	168	180	**2740**	1820	2950	1710	**214**	**766**
9	86	429	130	-104	-914	-301	217	-215	*	2230	2250	**-323**	**-974**
10	-229	134	-25	-59	-230	-230	-119	430	240	**2860**	2390	**166**	**886**
11	51	-12	-426	387	190	-91	21	-640	433	88	**2120**	**-7**	**146**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMP 91059.**

*** indicates a missing value.**

Mean = 2120, SE(mean) = $\pm$34, SE(g_i) = $\pm$288, SE(V_i) = $\pm$262, SE(s_{ij}) = $\pm$245.

Appendix 2. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; Patancheru, 1993 rainy season.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**3960**	3500	3300	3690	3280	3200	3490	3360	3450	3550	3530	**79**	**578**
2	53	**3660**	3510	3710	3310	3350	3730	3680	2290	3260	3330	**3**	**278**
3	-354	-61	**3870**	3340	3770	3430	3730	3820	2960	3740	3920	**209**	**482**
4	196	292	-281	**3260**	3480	3270	3150	3370	2480	3640	3940	**48**	**-118**
5	-107	-5	249	127	**2940**	3430	2830	3400	2930	3290	3430	**-54**	**-440**
6	-163	63	-63	-64	199	**3290**	3160	3220	2440	3780	3660	**-75**	**-93**
7	35	345	142	-276	-497	-140	**3400**	3100	3130	3570	3880	**14**	**12**
8	-70	326	266	-24	106	-52	-261	**3440**	2780	3320	3450	**-15**	**61**
9	594	-493	-32	-350	206	-260	335	17	**2090**	3140	2780	**-584**	**-1296**
10	-50	-256	12	74	-176	337	43	-182	-205	**3290**	3730	**152**	**-96**
11	-135	-262	121	307	-102	145	276	-124	-222	-6	**4010**	**223**	**631**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 3370, SE(mean) = ±26, SE(g_i) = ±219, SE(V_i) = ±199, SE(s_{ij}) = ±187.

Appendix 3. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; Patancheru, 1994 dry season.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**2540**	2640	2930	2350	2350	2570	2620	2290	2400	2720	2560	**114**	**135**
2	96	**2330**	2440	2640	2330	2330	2370	2480	2250	2220	2590	**-13**	**-71**
3	319	-45	**2600**	2350	2340	2450	2520	2830	2120	2370	2550	**54**	**194**
4	-175	240	-117	**1940**	2400	2440	2200	2390	2230	2730	2410	**-32**	**-460**
5	-81	31	-34	113	**2300**	2010	2290	2390	2210	2490	2480	**-125**	**-108**
6	107	-10	41	118	-215	**2540**	2420	2350	1850	2430	2770	**-88**	**140**
7	66	-57	26	-210	-20	72	**2240**	2390	2490	2380	2710	**-3**	**-158**
8	-316	2	289	-74	22	-57	-99	**2610**	2300	2720	2730	**51**	**206**
9	18	-6	-204	-6	60	-335	220	-25	**2150**	2450	2580	**-168**	**-250**
10	109	-262	-180	263	118	17	-117	177	119	**2440**	2410	**57**	**35**
11	-143	-10	-96	-153	6	262	119	82	157	-243	**2740**	**154**	**336**

[1] 1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2
6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.

Mean = 2430, SE(mean) = $\pm$23, SE(g_i) = $\pm$197, SE(V_i) = $\pm$179, SE(s_{ij}) = $\pm$168.

Appendix 4. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; Patancheru, 1994 rainy season.

	Parental populations (i = 1 to 11)												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**3350**	3530	3080	3590	3110	3430	3690	3480	2900	3900	3460	**168**	**295**
2	-68	**3450**	3500	3600	3560	3840	3060	3720	3010	3440	2910	**169**	**391**
3	-429	-4	**3270**	3900	3290	3230	2850	4010	2200	3470	3770	**72**	**209**
4	87	99	495	**2510**	3010	3150	2910	3400	2490	3100	4010	**66**	**-551**
5	-355	95	-81	-355	**3540**	3540	3110	3410	2570	4010	3200	**30**	**477**
6	132	339	26	-48	377	**2620**	2470	3000	1830	3480	3480	**-133**	**-439**
7	517	-113	-226	-163	76	-400	**2740**	3210	2530	2730	3730	**-260**	**-320**
8	-112	130	515	-91	-47	-290	49	**3190**	2640	3730	3480	**160**	**135**
9	262	336	-371	-75	41	-535	292	-17	**1940**	3240	2360	**-763**	**-1121**
10	169	-290	-162	-430	519	52	-564	8	447	**3320**	4010	**294**	**258**
11	-165	-722	337	480	-270	147	531	-144	-344	250	**3720**	**198**	**667**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 3230, SE(mean) = $\pm$40, SE(g_i) = $\pm$337, SE(V_i) = $\pm$306, SE(s_{ij}) = $\pm$287.

Appendix 5. Mean grain yield (kg ha^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean grain yield (kg ha^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; Patancheru, 1995 rainy season.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**3170**	3330	2790	3110	2670	2790	3140	3030	2940	2780	2860	**18**	**290**
2	400	**2770**	3270	2980	2450	2650	2800	2980	2820	3130	3060	**-18**	**-110**
3	-210	260	**3190**	3200	3200	3310	3300	2740	2300	3040	3030	**62**	**310**
4	110	-30	110	**3340**	3220	2940	3150	2830	2340	3140	3280	**63**	**460**
5	-270	-490	180	200	**2870**	3150	2860	3130	2660	3210	3040	**-6**	**-10**
6	-140	-280	300	-70	210	**2830**	2920	3070	2280	3230	3150	**-15**	**-50**
7	140	-210	210	60	-160	-90	**2920**	2770	2820	3160	3280	**62**	**40**
8	90	40	-280	-190	170	130	-250	**3170**	2530	3270	3250	**-1**	**300**
9	410	290	-310	-280	110	-260	210	-20	**1580**	2820	2390	**-411**	**-1300**
10	-330	20	-150	-50	90	120	-40	150	110	**2620**	3310	**168**	**-250**
11	-200	0	-110	140	-40	90	140	170	-280	70	**3200**	**115**	**320**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 2950, SE(mean) = $\pm$27, SE(g_i) = $\pm$229, SE(V_i) = $\pm$208, SE(s_{ij}) = $\pm$195.

Appendix 6. Mean growth index (GI) (g m^2 d^{-1}) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean growth index (GI) (g m^2 d^{-1}) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across two environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**8.0**	9.1	8.0	9.2	8.6	8.1	8.9	8.1	9.2	8.7	8.4	**-0.32**	**-0.94**
2	-0.8	**8.5**	8.3	9.3	8.5	8.2	8.8	7.8	9.6	9.2	8.0	**-0.25**	**-0.55**
3	-0.4	-0.1	**8.0**	8.4	9.2	8.4	9.4	8.6	9.6	8.4	9.0	**-0.20**	**-1.04**
4	0.3	0.3	-0.6	**8.6**	9.1	9.1	9.4	7.9	10.7	9.9	8.9	**0.30**	**-0.47**
5	0.2	0.0	0.6	0.1	**8.8**	9.5	8.2	8.6	8.6	9.0	8.3	**-0.18**	**-0.27**
6	-0.5	-0.4	-0.2	-0.1	0.8	**9.1**	8.9	8.0	10.3	10.1	8.3	**-0.04**	**0.03**
7	0.1	-0.1	0.5	0.0	-0.8	-0.3	**10.5**	9.1	9.7	9.5	9.4	**0.26**	**1.45**
8	-0.2	-0.5	0.2	-1.0	0.2	-0.5	0.2	**8.3**	9.9	9.8	8.6	**-0.30**	**-0.75**
9	-0.1	0.2	0.1	0.7	-0.9	0.6	-0.2	0.6	**12.4**	7.8	10.4	**0.70**	**3.41**
10	-0.1	0.3	-0.4	0.5	0.1	1.0	0.2	1.0	-2.0	**9.0**	8.4	**0.18**	**-0.04**
11	0.0	-0.5	0.4	-0.1	-0.3	-0.4	0.4	0.1	0.9	-0.5	**8.2**	**-0.16**	**-0.84**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 8.9, SE(mean) = $\pm$0.07, SE(g_i) = $\pm$0.58, SE(V_i) = $\pm$0.52, SE(s_{ij}) = $\pm$0.49.

Appendix 7. Mean time to flowering (days) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean biomass (days) (above diagonal) and specific combining ability effects (s_{ij},below diagonal) for their 55 crosses; across five environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**46**	51	49	51	51	53	54	50	56	48	47	**-2.9**	**-8.1**
2	0.5	**52**	50	53	53	55	56	50	57	53	52	**-0.6**	**-2.1**
3	1.4	0.5	**50**	51	51	54	53	49	54	49	49	**-3.1**	**-4.9**
4	-0.6	-0.1	0.3	**56**	55	56	55	53	61	54	52	**0.5**	**1.2**
5	0.4	0.3	0.1	0.4	**54**	56	56	52	58	53	51	**0.1**	**-0.5**
6	-0.2	-0.3	0.6	-1.0	-0.5	**57**	60	54	61	56	54	**2.5**	**3.0**
7	0.6	-0.4	-0.8	-2.1	-0.4	0.5	**59**	57	64	55	54	**3.1**	**5.0**
8	0.9	-1.3	-0.1	0.0	-0.1	-0.7	1.4	**52**	56	52	51	-1.3	-2.0
9	-0.1	-0.6	-1.6	1.5	-0.7	0.4	2.2	-1.2	**70**	57	57	**5.0**	**15.8**
10	-1.3	0.7	-0.7	1.3	0.6	1.3	-0.6	0.4	-0.7	**52**	49	**-1.0**	**-2.0**
11	-1.6	0.8	0.3	0.3	0.0	0.1	-0.5	0.7	0.9	-1.1	**49**	**-2.2**	**-5.7**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 54, SE(mean) = $\pm$0.05, SE(g_i) = $\pm$0.38, SE(V_i) = $\pm$0.35, SE(s_{ij}) = $\pm$0.33.

Appendix 8. Mean plant height (cm) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean plant height (cm) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across five environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**210**	225	215	220	225	240	240	215	245	215	210	**-12**	**-24**
2	3.5	**225**	220	235	230	245	240	230	240	235	230	**-3**	**-9**
3	2.7	1.2	**215**	230	220	230	240	215	240	220	210	**-12**	**-22**
4	-9.6	-4.3	3.6	**235**	235	255	250	240	265	240	230	**5**	**0**
5	3.6	-1.6	-0.5	-3.6	**230**	245	240	230	255	240	220	**-2**	**-6**
6	6.1	-0.5	-2.6	2.4	-1.4	**260**	255	235	270	245	230	**11**	**25**
7	3.9	-2.2	4.3	-2.5	-3.5	-1.4	**250**	245	265	245	240	**12**	**18**
8	-2.2	3.7	-1.6	3.2	1.0	-5.7	5.2	**240**	250	230	215	**-5**	**6**
9	1.2	-10.8	-4.0	4.8	1.1	5.4	-3.6	-0.1	**270**	250	250	**19**	**36**
10	-5.1	3.7	-1.0	3.2	6.8	0.6	-3.3	0.2	-0.7	**230**	220	**-1**	**-5**
11	-4.1	7.2	-2.5	2.7	-1.9	-3.0	2.7	-3.7	6.8	-4.3	**215**	**-11**	**-18**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 236, SE(mean) = $\pm$0.4, SE(g_i) = $\pm$3.4, SE(V_i) = $\pm$3.1, SE(s_{ij}) = $\pm$2.9.

Appendix 9. Mean panicle length (cm) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean panicle length (cm) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across five environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**25**	26	28	28	27	28	30	26	29	27	26	**-2.9**	**-5.1**
2	0.3	**27**	28	31	28	31	32	29	34	27	27	**-1.1**	**-3.8**
3	2.1	0.3	**28**	29	28	30	31	28	33	28	27	**-1.5**	**-2.4**
4	0.2	1.2	-0.5	**31**	30	31	32	28	40	29	28	**0.3**	**0.5**
5	0.1	-0.4	-0.1	0.2	**28**	32	31	28	39	29	27	**-0.3**	**-2.4**
6	-0.9	-0.4	-0.5	-1.2	0.0	**35**	36	30	41	31	29	**2.0**	**4.6**
7	0.0	-0.3	-0.8	-1.9	-1.6	1.3	**36**	32	42	32	30	**3.0**	**5.1**
8	0.1	1.2	0.4	-0.9	-0.6	-0.7	0.7	**28**	36	27	25	**-1.5**	**-2.2**
9	-4.6	-1.5	-2.2	2.8	2.4	3.0	2.6	0.6	**45**	34	32	**6.3**	**14.4**
10	1.2	-0.6	0.3	-0.3	0.4	0.0	0.5	-0.3	-1.2	**27**	26	**-1.4**	**-3.4**
11	1.6	0.4	1.1	0.4	-0.3	-0.6	-0.3	-0.5	-1.9	0.0	**25**	**-2.9**	**-5.3**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 30, SE(mean) = $\pm$0.1, SE(g_i) = $\pm$0.7, SE(V_i) = $\pm$0.6, SE(s_{ij}) = $\pm$0.6

Appendix 10. Mean tiller number (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean tiller number (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; across four environments in India.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**1.7**	1.8	1.6	1.8	1.6	1.5	1.6	1.7	1.5	1.8	1.7	**0.18**	**0.25**
2	0.06	**1.3**	1.7	1.7	1.8	1.4	1.3	1.4	1.4	1.7	1.5	**0.08**	**-0.20**
3	-0.10	0.08	**1.6**	1.5	1.7	1.5	1.3	1.8	1.3	1.6	1.6	**0.06**	**0.12**
4	-0.09	0.11	-0.08	**2.5**	1.7	1.3	1.4	1.4	1.2	1.5	1.6	**-0.01**	**1.03**
5	-0.22	0.08	-0.05	0.02	**1.4**	1.4	1.3	1.6	1.8	1.8	1.8	**0.18**	**-0.09**
6	-0.06	-0.02	0.08	-0.05	-0.01	**1.1**	1.3	1.3	1.0	1.3	1.5	**-0.17**	**-0.41**
7	0.09	-0.05	-0.05	0.08	-0.15	0.15	**1.1**	1.3	1.1	1.3	1.3	**-0.19**	**-0.35**
8	0.06	-0.16	0.22	-0.12	-0.03	0.03	0.04	**1.4**	1.3	1.4	1.6	**-0.02**	**-0.04**
9	0.00	0.08	-0.04	-0.04	0.35	-0.10	-0.01	0.02	**1.1**	1.3	1.1	**-0.22**	**-0.35**
10	0.07	0.02	-0.04	-0.09	0.07	-0.09	-0.04	-0.09	-0.03	**1.5**	1.8	**0.05**	**0.00**
11	-0.01	-0.19	-0.03	0.08	0.04	0.15	-0.06	0.03	-0.23	0.23	**1.5**	**0.06**	**0.06**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 1.5, SE(mean) = $\pm$0.01, SE(g_i) = $\pm$0.08, SE(V_i) = $\pm$0.08, SE(s_{ij}) = $\pm$0.07.

Appendix 11. Mean thousand seed mass (g) (on diagonal), general combining ability effects (g_i) and variety effects (V_i) for each of the eleven pearl millet populations and mean thousand grain weight (g) (above diagonal) and specific combining ability effects (s_{ij}, below diagonal) for their 55 crosses; Patancheru, 1995 rainy season.

	Parental populations (i = 1 to 11)[1]												
	1	2	3	4	5	6	7	8	9	10	11	g_i	V_i
1	**11.6**	11.8	11.7	10.8	9.7	10.4	10.8	10.6	10.0	11.6	10.9	**0.68**	**1.45**
2	0.85	**10.4**	10.7	9.9	9.8	10.1	9.2	10.6	9.7	10.6	10.6	**0.07**	**0.31**
3	0.25	-0.21	**11.4**	10.4	10.7	10.8	10.4	10.5	9.6	11.5	11.3	**0.57**	**1.28**
4	-0.05	-0.41	-0.28	**8.9**	9.8	9.7	10.4	11.0	9.6	10.1	9.8	**-0.10**	**-1.22**
5	-0.87	-0.16	0.23	0.04	**9.6**	10.3	9.6	10.4	8.5	9.9	10.4	**-0.15**	**-0.49**
6	-0.20	0.11	0.24	-0.12	0.69	**10.0**	8.6	10.8	9.0	9.3	10.7	**-0.28**	**-0.12**
7	0.60	-0.40	0.23	0.94	0.38	-0.68	**7.7**	9.8	7.9	9.7	9.8	**-0.68**	**-2.46**
8	-0.69	-0.08	-0.72	0.49	0.17	0.51	-0.13	**11.1**	10.2	11.1	10.7	**0.37**	**0.98**
9	0.07	0.35	-0.29	0.38	-0.41	0.00	-0.71	0.51	**9.5**	10.0	9.3	**-0.95**	**-0.59**
10	0.33	-0.07	0.40	-0.37	-0.29	-0.98	-0.16	0.13	0.36	**10.4**	11.5	**0.33**	**0.31**
11	-0.30	0.01	0.14	-0.62	0.22	0.43	-0.08	-0.19	-0.27	0.65	**10.7**	**0.32**	**0.55**

[1] **1 = ICMV 155, 2 = ICMP 87307, 3 = ICMP 91751, 4 = ICMP 87200, 5 = NWC C2, 6 = AfPop 88, 7 = AfPop 90, 8 = ICMP 92591, 9 = LHGP, 10 = SenPop, 11 = ICMV 91059.**

Mean = 10.2, SE(mean) = $\pm$0.05, SE(g_i) = $\pm$0.43, SE(V_i) = $\pm$0.39, SE(s_{ij}) = $\pm$0.36.

Appendix 12. Computer program for statistical analysis of an eleven parent diallel (parents and 55 hybrids without reciprocals) using Genstat Version 4 for the Analysis II of Gardner and Eberhart (1966).

```
'REFE/NUNN=1000,NID=1000' DIALLEL_ANALYSIS_GARDNER_AND_EBERHART_METHOD
'UNITS' $ 396
'SCAL' CRS=66 : NREP=3 : DSIZE=11 : NLOC=2 'SCAL' MF
'FACT' CROS $ CRS=(1...CRS)6 : REP $ NREP : LOC $ NLOC=198(1...NLOC)
'CALC' MF=DSIZE*DSIZE
'SCAL' NV=4
'INTE' NUM_VAR=1...NV
'INPU/RECL=132' 2
'READ/P' REP,DDENT,VARIABLE(NUM_VAR)
'INPUT' 1
'R'
'SCAL' OBS,N,K,EDF,ESS,EMS
'VARI' TRTMN $ CRS
'FOR' YSET=VARIABLE(NUM_VAR)
'FOR' J=1...CRS
'REST' YSET $ CROS=J
'CALC' K=MEAN(YSET)
'COPY' TRTMN $ J=K
'REPE'
'REST' YSET
'BLOC' LOC.REP/CROS
'TREAT' LOC*CROS
'ANOV/PR=10,PROB=Y' YSET ; OUT=AOV1
'EXTR' AOV1 ; LOC.REP.CROS $ SS=ESS ; DF=EDF
'CALC' EMS=ESS/EDF
'CALC' EMS=EMS/(NLOC*NREP)
'VARI' REPMN $ MF
'SCAL' K1,K2,K3 'CALC' K1=1 : K2=1 : K3=1
'SCAL' IJ,IK1,IK2,IK3
'FOR' I=1...DSIZE : J=1...DSIZE
'CALC' IJ=J+DSIZE*(I-1)
'JUMP' LB1*(I.EQ.J)
'JUMP' LB2*(I.LT.J)
'JUMP' LB3*(I.GT.J)
'LABE' LB1
'EQUA' IK1=K1
'COPY' REPMN $ IJ=TRTMN $ IK1
'CALC' K1=K1+DSIZE-I+1
'JUMP' LB4
```

```
'LABE' LB2
'CALC' IK2=K2+1
'COPY' REPMN $ IJ=TRTMN $ IK2
'CALC' K2=K2+1
'JUMP' LB4
'LABE' LB3
'CALC' IK3=K3+1
'COPY' REPMN $ IJ=TRTMN $ IK3
'CALC' K3=K3+DSIZE-J
'LABE' LB4
'REPE'
'CALC' K2=K2+1 : K3=I
'REPE'
'SCAL' YDD,PM,MU,ZDD,HB,SEMU,SEHB,SEVI,SEVIJ,SEHI,SEHIJ,SESIJ,SESIJCK,SESIJKM,
     SSENT,SSVAR,SSVJ,SSG4,SSS4,SSHB,SSHIJ,SSHJ,DFENT,DFVAR,DFVJ,DFG4,
     DFS4,DFHB,DFHIJ,DFHJ,MSENT,MSVAR,MSVJ,MSG4,MSS4,MSHB,MSHIJ,MSHJ,
     FENT,FVAR,FVJ,FG4,FS4,FHB,FHIJ,FHJ
'VARI' Y1,Y2,YII,YIDOT,REPMNS(1...DSIZE),VI,HI $ DSIZE
'MATR' REPMNMA,YIIMAT,YIIMATS,YIIMA,SIJC $ DSIZE,DSIZE
'SYMM' SIJ,MATREP $ DSIZE
'DIAG' YIIS,SIJD $ DSIZE
'EQUA' REPMNMA=REPMN
'CALC' MATREP=REPMNMA
'HEAD' H12='' MEAN DATA OVER REPLICATIONS
'LINE' 5
'PRINT' H12
'LINE' 2
'PRINT/LABR=1,LABC=1' MATREP $ 8.3
'CALC' YDD=SUM(TRTMN)
'CALC' YIIS=REPMNMA
'EQUA' YII=YIIS
'CALC' PM=SUM(YII)
'EQUA' REPMNS(1...DSIZE)=REPMNMA
'CALC' YIDOT=VSUM(REPMNS(1...DSIZE))
'CALC' Y1=YIDOT-YII : Y2=YIDOT+YII
'CALC' ZDD=SUM(Y1)/2
'CALC' MU=(2*YDD)/(DSIZE*(DSIZE+1))
'CALC' VI=( YII-(PM/DSIZE) )
'CALC' HB=(2*ZDD)/(DSIZE*(DSIZE-1))
'CALC' HB=HB-(PM/DSIZE)
'CALC' HI=( YIDOT-(DSIZE*YII/2) )
'CALC' HI=HI + ( ( (DSIZE-2)/(2*DSIZE) )*PM - (2/DSIZE)*ZDD )
'CALC' HI=HI/(DSIZE-2)
```

```
'EQUA' YIIMAT=Y1
'CALC' YIIMATS=TRANS(YIIMAT)
'CALC' YIIMA=YIIMAT+YIIMATS
'CALC' SIJC=REPMNMA-(YIIMA/(DSIZE-2))+((2*ZDD)/((DSIZE-1)*(DSIZE-2)))
'CALC' SIJD=SIJC
'CALC' SIJC=SIJC-SIJD
'CALC' SIJ=SIJC
'CALC' SEMU=SQRT( (2*EMS)/(DSIZE*(DSIZE+1)) )
'CALC' SEVI=SQRT( ((DSIZE-1)*EMS)/DSIZE )
'CALC' SEVIJ=SQRT( 2*EMS )
'CALC' SEHB=SQRT( ((DSIZE+1)*EMS)/(DSIZE*(DSIZE-1)) )
'CALC' SEHI=(DSIZE-1)*(DSIZE+2)/(4*DSIZE*(DSIZE-2))
'CALC' SEHI=SQRT(SEHI*EMS)
'CALC' SEHIJ=SQRT( ((DSIZE+2)*EMS)/(2*(DSIZE-2)) )
'CALC' SESIJ=SQRT( ((DSIZE-3)*EMS)/(DSIZE-1) )
'CALC' SESIJCK=SQRT( (2*(DSIZE-3)*EMS)/(DSIZE-1) )
'CALC' SESIJKM=SQRT( (2*(DSIZE-4)*EMS)/(DSIZE-2) )
'CALC' SSENT=SUM(TRTMN*TRTMN)
'CALC' SSENT=SSENT-( (2*YDD*YDD)/(DSIZE*(DSIZE+1)) )
'CALC' SSVAR=SUM(YII*YII)-(PM*PM/DSIZE)
'CALC' SSVJ=( SUM(Y2*Y2)/(DSIZE+2) )-( (4*YDD*YDD)/(DSIZE*(DSIZE+2)) )
'CALC' SSG4=( SUM(Y1*Y1)/(DSIZE-2) )-( (4*ZDD*ZDD)/(DSIZE*(DSIZE-2)) )
'CALC' SSS4=( SUM(TRTMN*TRTMN)-SUM(YII*YII) )
'CALC' SSS4=SSS4-( SUM(Y1*Y1)/(DSIZE-2) )+( (2*ZDD*ZDD)/((DSIZE-1)*(DSIZE-2)) )
'CALC' SSHB=(2*ZDD*ZDD)/(DSIZE*(DSIZE-1))
'CALC' SSHB=SSHB+(PM*PM/DSIZE)-( (2*YDD*YDD)/ (DSIZE*(DSIZE+1)) )
'CALC' SSHIJ=SSENT-SSVJ
'CALC' SSHJ=SSHIJ-SSHB-SSS4
'CALC' DFENT=(DSIZE*(DSIZE+1)/2)-1 : DFVAR=DSIZE-1: DFVJ=DSIZE-1 : DFG4=DSIZE-1
'CALC' DFS4=DSIZE*(DSIZE-3)/2 : DFHB=1 : DFHIJ=DSIZE*(DSIZE-1)/2 : DFHJ=DSIZE-1
'CALC' MSENT=SSENT/DFENT : MSVAR=SSVAR/DFVAR : MSVJ=SSVJ/DFVJ : MSG4=SSG4/DFG4
'CALC' MSS4=SSS4/DFS4 : MSHB=SSHB/DFHB : MSHIJ=SSHIJ/DFHIJ : MSHJ=SSHJ/DFHJ
'CALC' FENT=MSENT/EMS : FVAR=MSVAR/EMS : FVJ=MSVJ/EMS : FG4=MSG4/EMS
'CALC' FS4=MSS4/EMS : FHB=MSHB/EMS : FHIJ=MSHIJ/EMS : FHJ=MSHJ/EMS
'HEAD' H1=
"SOURCE              DF          SS          MS        F "
'HEAD' H2="Entries          "
'HEAD' H3="Varieties (v(j))  "
'HEAD' H4="Heterosis (h(ij)) "
'HEAD' H5="Average (hb)      "
'HEAD' H6="Variety (h(j))    "
'HEAD' H7="Specific (s(ij))  "
'HEAD' H8="Residual          "
```

```
'LINE' 3
'PRINT' H1
'LINE' 2
'PRINT/C,LABR=1,LABC=1' H2,DFENT,SSENT,MSENT,FENT $ 0,20,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H3,DFVJ,SSVJ,MSVJ,FVJ $ 0,11,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H4,DFHIJ,SSHIJ,MSHIJ,FHIJ $ 0,10,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H5,DFHB,SSHB,MSHB,FHB $ 0,15,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H6,DFHJ,SSHJ,MSHJ,FHJ $ 0,13,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H7,DFS4,SSS4,MSS4,FS4 $ 0,11,19.3,17.3,12.2
'PRINT/C,LABR=1,LABC=1' H8,EDF,ESS,EMS $ 0,19,19.3,17.3
'LINE' 2
'PRIN' MU $ 12.3
'PRINT' VI $ 12.3
'PRIN' HB $ 12.3
'PRIN' HI $ 12.3
'PRIN' SIJ $ 12.3
'LINE' 2
'HEAD' H13=" SE ( mu )          "
'HEAD' H14=" SE ( v(i) )        "
'HEAD' H15=" SE ( v(i)-v(j) )   "
'HEAD' H16=" SE ( hb )          "
'HEAD' H17=" SE ( h(i) )        "
'HEAD' H18=" SE ( h(i)-h(j) )   "
'HEAD' H19=" SE ( s(ij) )       "
'HEAD' H20=" SE ( s(ij)-s(ck) ) "
'HEAD' H21=" SE ( s(ij)-s(km) ) "
'PRIN/C,LABR=1,LABC=1' H13,SEMU $ 0,19.4
'PRIN/C,LABR=1,LABC=1' H14,SEVI $ 0,17.4
'PRIN/C,LABR=1,LABC=1' H15,SEVIJ $ 0,12.4
'PRIN/C,LABR=1,LABC=1' H16,SEHB $ 0,19.4
'PRIN/C,LABR=1,LABC=1' H17,SEHI $ 0,17.4
'PRIN/C,LABR=1,LABC=1' H18,SEHIJ $ 0,12.4
'PRIN/C,LABR=1,LABC=1' H19,SESIJ $ 0,16.4
'PRIN/C,LABR=1,LABC=1' H20,SESIJCK $ 0,10.4
'PRIN/C,LABR=1,LABC=1' H21,SESIJKM $ 0,10.4
'DEVAL' REPMNMA,YIIMAT,YIIMATS,YIIMA,SIJC,SIJ,MATREP,YIIS,SIJD
'REPE'
'R'
'CLOS'
'STOP'
```